National Research Council Canada

Conseil national de recherches Canada

NRC·CNRC

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

http://cjfas.nrc.ca

http://jcsha.cnrc.ca

ISSN 0706-652X / CJFSDX 60(8) 897–1037 (2003)

The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy. The Journal publishes original research articles, perspectives (syntheses, critiques, re-evaluations), discussions (comment and reply), and rapid communications. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results. The Journal encourages papers that lead from clearly stated purpose or rationale and from testable hypotheses, concepts, or questions to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. The Journal discourages papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); only confirm previously established principles; or apply standard techniques without breaking new methodological ground.

Manuscripts for publication should be submitted to the Senior Editor, *Canadian Journal of Fisheries and Aquatic Sciences*, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 ext. 52646; fax: 519-767-9798; e-mail: cjfas@uoguelph.ca).

Submissions in either English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor.

Correspondence concerning accepted manuscripts and corrected proofs should be sent to NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada (fax: 613-952-7656; e-mail: research.press@nrc.gc.ca).

Instructions to Authors are published once a year in the first issue of each volume. Copies are available from NRC Research Press or at http://cjfas.nrc.ca. The **Publication Policy** of NRC Research Press is available at http://cjfas.nrc.ca.

Microfilm. Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, U.S.A.

U.S. periodical postage paid at Champlain, N.Y., and at additional mailing offices. Attention U.S. POSTMASTER: Send address changes to **Canadian Journal of Fisheries and Aquatic Sciences**, c/o USACAN Media Distribution Center, P.O. Box 2888, Plattsburg, NY 12901, U.S.A.

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, et *Journal of the Fisheries Research Board of Canada* 1938–1979. Le Journal paraît tous les mois, formant ainsi un volume de 12 numéros, et offre en plus jusqu'à deux suppléments par année.

Politique éditoriale. On publie, dans le Journal, des articles rendant compte de recherche originale, des perspectives (synthèses, critiques et réévaluations), des discussions (commentaires et réponses) et des communications rapides. Les documents peuvent porter sur les cellules, organismes, populations, communautés, écosystèmes ou processus qui affectent les systèmes aquatiques. Ils peuvent relever de divers domaines y compris la biologie et l'écologie des organismes marins et d'eau douce, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, la pathologie et la gestion. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux. On invite les auteurs à soumettre des articles ayant des objectifs précis ou relevant d'hypothèses, de concepts ou de questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. On décourage toutefois la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicables à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie.

Les auteurs voudront adresser leurs **manuscrits** à la directrice scientifique principale, *Journal canadien des sciences halieutiques et aquatiques*, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 poste 52646; télécopieur : 519-767-9798; courriel : cjfas@uoguelph.ca).

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à.-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le CNRC ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations qui pourrait faire ce dernier.

La correspondance ayant trait aux manuscrits acceptés et les **épreuves corrigés** doivent être envoyées aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada (télécopieur : 613-952-7656; courriel : presses.scientifiques@cnrc.gc.ca).

Les Recommandations aux auteurs sont publiées une fois par année dans le premier numéro de chaque volume. Des copies sont disponibles auprès du Bureau de la rédaction aux Presses scientifiques du CNRC ou au http://jcsha.cnrc.ca. **La Politique de publication** est disponible auprès des Presses scientifiques du CNRC ou au http://jcsha.cnrc.ca.

Microfilms. On peut acheter sur microfilms de 16 ou 35 mm tous les numéros depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, É.-U.

This Journal is indexed or abstracted in / Cette revue est signalée ou résumée dans
ABSEARCH, Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Biological & Agricultural Index, CAB Abstracts, Chemical Abstracts, Current Contents, Elsevier BIOBASE, Environmental Abstracts, Environmental Periodicals Bibliography, GEOBASE, GeoRef, Internationale Bibliographie der Zeitschriftenliteratur, Life Sciences Collection, Meteorological and Geoastrophysical Abstracts, Oceanic Abstracts, PASCAL Database, and Science Citation Index.

Volume 60, Number 8, August 2003

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 60, numéro 8, août 2003

Journal canadien des sciences halieutiques et aquatiques

Publié par le Conseil national de recherches du Canada

Senior Editor / Directrice scientifique principale **Moira M. Ferguson**

Editors / Directeurs

Jeffrey A. Hutchings, *Dalhousie University, Halifax*
Pierre Pepin, *Northwest Atlantic Fisheries Centre, DFO/MPO, St. John's, Newfoundland*
W. Gary Sprules, *University of Toronto at Mississauga*
Assistant to the Editors / Adjointe aux directeurs scientifiques **Holly Foster**

Associate Editors / Directeurs scientifiques associés

M.T. Arts, *Environment Canada, Burlington*
D. Boisclair, *Université de Montréal*
U. Borgmann, *Environment Canada, Burlington*
S.E. Campana, *DFO/MPO, Dartmouth*
R. Carignan, *Université de Montréal*
J.J. Dodson, *Université Laval*
G.T. Evans, *DFO/MPO, St. John's, Newfoundland*
K.T. Frank, *DFO/MPO, Dartmouth*
M.M. Hansen, *Danish Institute for Fisheries Research, Silkeborg, Denmark*
R. Hilborn, *University of Washington*
A. Hontela, *Université du Québec à Montréal*
D.F. Houlihan, *University of Aberdeen*
F.A. Huntingford, *University of Glasgow*
G.S. Jamieson, *DFO/MPO, Nanaimo*
B. Jonsson, *Norwegian Institute for Nature Research, Oslo, Norway*
P. Magnan, *Université du Québec à Trois Rivières*
C.T. Marshall, *University of Aberdeen*
R.B. Millar, *University of Auckland, New Zealand*
Y.T. Prairie, *Université du Québec à Montréal*
T.J. Quinn II, *University of Alaska–Fairbanks, Juneau, Alaska*
T.P. Quinn, *University of Washington*
R.D. Robarts, *Environment Canada, Saskatoon*
B. Sainte-Marie, *DFO/MPO, Mont-Joli*
D.W. Schindler, *University of Alberta*
R.E.H. Smith, *University of Waterloo*
S.J. Smith, *DFO/MPO, Dartmouth*
W.F. Vincent, *Université Laval*
R.D. Vinebrooke, *University of Regina*
C.J. Walters, *University of British Columbia*
R.D. Ward, *CSIRO Marine Research, Australia*
B. de Young, *Memorial University of Newfoundland*

NRC Research Press / Presses scientifiques du CNRC

Editor-in-chief / Directeur général **Bruce P. Dancik**
Assistant Editor-in-chief / Directeur général adjoint **Iain E.P. Taylor**

Journals Program / Programme des revues

(Fax / Télécopieur : 613-952-7656; e-mail: research.press@nrc.gc.ca / courriel : presses.scientifiques@cnrc.gc.ca; URL: http://pubs.nrc-cnrc.gc.ca)
Director / Directrice **Aldyth Holmes**
Business Manager / Gestionnaire des affaires **Paul McClymont**
Manager, Journals Program / Gestionnaire, Programme des revues **Carolyn Brown**
Managing Editor / Rédactrice administrative **Cecily M. Pearson** (613-993-9099)
Publication Officers / Agentes de publication **Jennifer McColl and Lee Murphy**
Advertising / Annonces publicitaires **Judy Gorman** (613-993-0151)
Reprints / Tirés à part **Roxanne Landriault** (613-990-2254)
Subscriptions / Abonnements **Eileen Evans-Nantais** (613-990-7873)

The National Research Council of Canada accepts no responsibility for statements or opinions expressed by a contributor. Acceptance of an advertisement, announcement, or other material does not imply endorsement by either the Journal's Senior Editor or the National Research Council.

© National Research Council of Canada 2003. All rights reserved.

No part of this publication may be reproduced, stored, or transmitted in any form or by any means, without the written permission of the publisher, except as stated below.

The National Research Council of Canada grants **permission*** to individuals to make single copies of articles for personal use. Any person may reproduce short excerpts from articles in the journal for any purpose that respects the moral rights of authors, provided that the source is fully acknowledged. As a courtesy, the consent of authors of such material should be obtained directly from the author.

Authorization to reproduce items for other than personal use, as stated above, is granted by the National Research Council of Canada provided that the copyright fee of $7.00 per copy is paid directly to CANCOPY, One Yonge Street, Suite 1900, Toronto, ON M5E 1E5, Canada.

*The above permission does not extend to other kinds of copying, such as copying for general distribution, for advertising, or promotional purposes, for creating new collective works, or for resale. For such copying, arrangements must be made with the publisher, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Subscription information

The *Canadian Journal of Fisheries and Aquatic Sciences* (ISSN 0706-652X) is published monthly by the National Research Council of Canada. The 2003 annual subscription rates (second class postage) for Canada are $830CAN institutional and $257CAN personal, for US & foreign $830US institutional and $257US personal. For air mail add $175US to foreign rate. Canadian customers please include 7% GST (business no. 12149 1807 RT 0275). Subscriptions are entered for the calendar year. Remittances should be made payable to the Receiver General for Canada credit NRC. Price for regular single issues: institutional, $105.00; personal, $35.00. Supplements will be priced separately. Special rates apply to members of Canadian scientific and engineering societies if they subscribe through their respective societies.

There are no refunds on cancelled subscriptions once delivery has begun. Claims for missing issues should be made within four months (N. America) or six months (outside N. America) following the date of publication. The publisher expects to supply missing issues only when losses have occurred in transit and when the reserve stock will permit. For change of address and subscription enquiries: Subscription Office, NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada; tel.: 613-993-9084; fax: 613-952-7656; e-mail: research.press@nrc.gc.ca.

Microform backfiles are available from UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, U.S.A., and Micromedia Ltd., 20 Victoria St., Toronto, ON M5C 2N8, Canada.

All issues of the *Canadian Journal of Fisheries and Aquatic Sciences* since 1996 are available on the Web. Pricing information can be found at http://cjfas.nrc.ca.

Le Conseil national de recherches du Canada ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations que pourrait faire ce dernier. La publication d'annonces publicitaires, d'avis et autres n'implique pas l'endossement de leur contenu par la directrice principale de la Revue ou le CNRC.

© Conseil national de recherches du Canada 2003. Tous droits réservés.

Il est interdit de reproduire, de sauvegarder ou de transmettre quelque partie de la présente publication dans quelque format ou de quelque façon sans le consentement écrit de l'éditeur, à l'exception des conditions suivantes.

Le Conseil national de recherches du Canada accorde aux particuliers le droit de faire des copies individuelles pour leur usage personnel. Toute personne peut reproduire de courts extraits des articles de la Revue pour autant que les droits moraux de l'auteur soient respectés et que la mention de provenance soit clairement indiquée. Il est de convenance de demander le consentement de l'auteur avant de faire mention de son travail.

On obtiendra l'autorisation de reproduire des articles à d'autres fins que l'usage personnel (tel qu'on l'a décrit ci-dessus) auprès du Conseil national de recherches du Canada pour autant que des redevances de droits d'auteurs de 7,00 $/copie soient versées au CANCOPY, 1, rue Yonge, bureau 1900, Toronto, ON M5E 1E5, Canada.

*La permission ci-dessus ne s'applique pas à la reproduction à grande échelle, telle que la reproduction aux fins de distribution générale, publicitaire ou promotionnelle, de compilation de nouveaux ouvrages collectifs ou de revente. Dans de tels cas, il faudra ratifier une entente particulière avec l'éditeur, le Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Renseignements sur l'abonnement

Journal canadien des sciences halieutiques et aquatiques (ISSN 0706-652X) est une publication mensuelle du Conseil national de recherches du Canada. Le prix de l'abonnement annuel au Canada (courrier de deuxième classe) est de 830 $CAN pour les organismes et de 257 $CAN pour les particuliers. À l'étranger (y compris les É.-U.), le prix de l'abonnement est de 830 $US pour les organismes et de 257 $US pour les particuliers. L'expédition par avion exige des frais de 175 $US en sus du prix d'abonnement à l'étranger. Les clients du Canada doivent ajouter la TPS de 7% (numéro d'entreprise 12149 1807 RT 0275). Les abonnements sont pour l'année civile. Tout paiement doit être adressé au Receveur général du Canada, crédit du CNRC. Le prix par numéro est de 105 $ pour les organismes et de 35 $ pour les particuliers. Le prix des hors-série varie. Les membres des sociétés canadiennes de sciences et de génie bénéficient de taux préférentiels en s'abonnant via leurs sociétés respectives.

Aucun remboursement ne sera accordé ni aucune annulation acceptée une fois que les livraisons auront commencé. Les réclamations de numéros manquants devront être soumises dans les quatre mois (Amérique du Nord) ou dans les six mois (à l'extérieur de l'Amérique du Nord) suivant la date de publication. L'éditeur ne fournira de numéros manquants que si le document a été perdu pendant l'expédition et que si le stock le permet. Adressez tout changement d'adresse ou toute question quant à l'abonnement au : Bureau des abonnements, Presses scientifiques du CNRC, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada; téléphone : 613-993-9084; télécopieur : 613-952-7656; courriel : presses.scientifiques@cnrc.gc.ca.

On peut obtenir les fichiers rétrospectifs sur **microforme** auprès de UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, É.-U., et auprès de Micromedia Ltée, 20, rue Victoria, Toronto, ON M5C 2N8, Canada.

À partir de 1996, tous les numéros de *Journal canadien des sciences halieutiques et aquatiques* sont accessibles sur le Web. On trouvera des renseignements sur les tarifs à http://jcsha.cnrc.ca.

Spatial distribution of catch and effort in a fishery for snow crab (*Chionoecetes opilio*): tests of predictions of the ideal free distribution

Douglas P. Swain and Elmer J. Wade

Abstract: The ideal free distribution (IFD), a hypothesis from behavioural ecology, predicts that fishery effort should map resource distribution better than catch-per-unit-effort (CPUE) when interference competition occurs in the fishery. We tested this prediction using data from the fishery and annual research survey for snow crab (*Chionoecetes opilio*) in the southern Gulf of St. Lawrence. Effort was positively correlated with the local abundance of crabs in all years. Correlations between CPUE and local crab abundance were also positive in some years, but negative in others. In the latter cases, CPUE and effort were also negatively correlated, suggesting intense competition in the fishery. In most years, CPUE tended to be equalized among areas compared with the distributions of effort and local crab abundance, as predicted by the IFD. In most years, differences in spatial distribution were more significant between CPUE and crab abundance than between effort and crab abundance. Although effort was the more reliable indicator of resource distribution, even it provided a distorted view of this distribution, as predicted given expected violations of IFD assumptions. For example, effort tended to be higher than expected on fishing grounds near home ports and lower than expected on distant grounds.

Résumé : La distribution libre idéale (IFD), une hypothèse provenant de l'écologie comportementale, prédit qu'on peut mieux établir la répartition géographique d'une ressource halieutique à partir des efforts de pêche qu'avec les captures par unité d'effort (CPUE) lorsqu'il existe une compétition par interférence dans une pêche commerciale. Nous avons vérifié cette prédiction avec des données provenant de la pêche commerciale et d'un relevé de recherche annuel du crabe des neiges (*Chionoecetes opilio*) dans le sud du golfe du Saint-Laurent. Toutes les années, l'effort de pêche est en corrélation positive avec l'abondance locale des crabes. Les corrélations entre CPUE et l'abondance locale de crabes sont aussi positives certaines années, mais négatives d'autres années. Dans ces derniers cas, CPUE et l'effort de pêche sont aussi en corrélation négative, ce qui laisse croire à une compétition intense dans la pêche commerciale. La plupart des années, CPUE tend à être plus égal d'une région à l'autre que les efforts de pêche ou l'abondance locale des crabes, comme le prédit l'hypothèse IFD. La plupart des années, les différences de répartition spatiale tendent à être plus significatives entre CPUE et l'abondance des crabes qu'entre l'effort de pêche et l'abondance des crabes. Bien que l'effort de pêche soit l'indicateur le plus fiable de la répartition de la ressource, il procure une image déformée de cette répartition, comme on peut s'y attendre car toutes les conditions préalables de l'IFD risquent de ne pas être remplies. Par exemple, les efforts de pêche tendent à être plus intenses que prévu sur les sites pêches près des ports d'attache et à l'être moins que prévu dans les endroits plus éloignés.

[Traduit par la Rédaction]

Introduction

Information about the abundance and distribution of exploited fish populations comes primarily from research surveys and the fisheries themselves. Catch-per-unit-effort (CPUE) in fisheries is often used as an index of fish abundance. However, interpretation of fishery CPUE as an index of abundance is complicated by systematic variation in catchability, the proportion of the population removed by a unit of fishing effort. Catchability to fisheries often increases over time as a result of technological improvements (e.g., Garrod 1964; Gulland 1964) and is expected to be density-dependent, increasing as population size decreases and geographic range contracts (e.g., Paloheimo and Dickie 1964; Rose and Leggett 1991; Harley et al. 2001). Survey catch rates are expected to be free of these difficulties, because the same standard methods and gear are used each year and fishing is conducted at random in relation to fish distribution. However, for most stocks, surveys provide at most a single annual "snapshot" of fish distribution during one part of the year, and information on distribution in other seasons must be derived from fishery catch and effort data.

An understanding of relationships between fishery catch rates and the local abundance of fish is needed to infer fish distribution from fishery data. The relationship between CPUE and local abundance may break down in the presence of interference competition (Gillis et al. 1993; Gillis and

Received 8 October 2002. Accepted 4 June 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 September 2003.
J17137

D.P. Swain[1] and E.J. Wade. Department of Fisheries and Oceans, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.

[1]Corresponding author (e-mail: SwainD@dfo-mpo.gc.ca).

 doi: 10.1139/F03-076 © 2003 NRC Canada

Peterman 1998). Interference competition refers to rapidly reversible decreases in foraging efficiency resulting from interactions between foragers. In fisheries, interference could result from factors such as gear entanglement, competition for space on the best fishing grounds, and temporary dispersal of fish. The rare tests for interference between fishing vessels have produced mixed results. In a manipulative field experiment, Abrahams and Healey (1993) found that catch rates declined for chinook salmon (*Oncorhynchus tshawytscha*) but increased for spiny dogfish (*Squalus acanthias*) when troll vessels fished in closer proximity. A relationship between course linearity and vessel density indicated that interference competition occurred in the trawl fishery for silver hake (*Merluccius bilinearis*) on the Scotian Shelf (Gillis 1999). Analysis of catch and effort data provided evidence for interference competition in the bottom-trawl fishery in Hecate Strait, British Columbia (Gillis et al. 1993), but not in the New Zealand hoki (*Macruronus novaezelandiae*) fishery (Vignaux 1996).

Gillis et al. (1993) examined fleet dynamics in the Hecate Strait bottom-trawl fishery using the ideal free distribution (IFD), a hypothesis from behavioural ecology that predicts the distribution of foragers and foraging success between areas (Fretwell and Lucas 1970; Fretwell 1972). The theory assumes that foragers have ideal knowledge of the distributions of resources and other foragers, that they are free to move between areas without costs, that competition occurs among foragers in proportion to their local density, and that all foragers have equal competitive abilities. The IFD predicts that foragers will distribute themselves among areas so that foraging success or profit rate is the same in all areas. In this situation, forager density will reflect local resource abundance better than profit rate. In spite of its unrealistic assumptions, the IFD often performs well in predicting the distribution of forgers (see references in Gillis et al. 1993). Gillis et al. (1993) found evidence that CPUE was equalized among areas in the Hecate Strait trawl fishery and suggested that fishing effort may provide a better indication of local fish abundance than CPUE in this fishery. Gillis and Peterman (1998) developed an alternative index of local abundance, based on the distribution of effort between areas, for cases in which interference occurs between fishing vessels.

In previous studies, it has not been possible to directly test IFD predictions by comparing the spatial distribution of fishery effort or CPUE with local fish abundance because fishery-independent indices of local abundance were not available. Annual research surveys provide information on the spatial distribution of many commercially important finfishes. However, these fishes are typically highly mobile and migratory, and it is not possible to infer their distribution during fisheries from surveys conducted at other times of the year. Large commercially important benthic invertebrates (e.g., crabs) are typically less mobile than the commercially important finfishes. In this paper, our purpose is to compare survey-based measures of local resource abundance with the spatial distributions of fishery effort and CPUE for snow crab (*Chionoecetes opilio*) in the southern Gulf of St. Lawrence. We show that estimates of the spatial distribution of crabs from a postfishery survey in one year are closely correlated with estimates based on fishery removals and the postfishery survey in the next year. We thus compare these survey-based estimates of local crab abundance with the spatial distribution of fishery effort and CPUE to test the IFD prediction that effort should provide a better indication of local resource abundance than fishery CPUE.

Material and methods

The fishery

A trap fishery for snow crab has been conducted in the southern Gulf of St. Lawrence since the mid-1960s. The fishery is managed separately in each of several zones (Fig. 1), with the largest fishery in zone 12. Analyses presented here are restricted to the zone 12 fishery. The fishery in this zone opens in spring, generally as soon as the area is clear of ice (April–May), and lasts about 10–12 weeks. This fishery has been traditionally conducted by 130 midshore fishermen limited to 150 traps per license and 30 fishermen operating in coastal waters off Prince Edward Island (P.E.I.) with a limit of 50 traps per license. In most years since 1995, a portion of the quota (11–23%) has been allocated to additional "nontraditional" vessels. Before 1990, the fishery was competitive, with an overall quota and no limit to the proportion of the quota taken by individual fishermen. Since then, each fisherman has been allocated an individual quota.

Male snow crab undergo a final or "terminal" molt at sizes ranging from 40 to 160 mm carapace width (CW; Conan and Comeau 1986; Sainte-Marie and Hazel 1992). Terminally molted males are referred to here as adult males (Sainte-Marie et al. 1995). Molting occurs in December–April (Hébert et al. 2002*a*), before the fishery. After molting, crabs have a soft shell for 8–10 months (Hébert et al. 2002*a*). Only adult hard-shelled males with CW ≥95 mm can be landed in the fishery. Terminally molted soft-shelled males with CW ≥95 mm will be recruited to the fishery the next year.

Data on the spatial distributions of catch and effort were obtained from fishermen's logbooks and the sales slips of processing plants. Effort (number of traps) and catch (kg) were summed within 10-min grids (Fig. 2) for the entire fishing season in each year from 1990 to 2001. Over 95% of the catch and effort data in each year could be identified to grid. CPUE was estimated for each grid by dividing the catch in a grid by the number of traps fished in the grid (summed over all fishing trips in a year).

The survey

A trawl survey for snow crab has been conducted after the fishing season in zone 12 each year since 1988 (except in 1996) using the same standardized procedures (see details in Hébert et al. 2002*b*). The survey follows a systematic design, with one or two stations fished within each 10-min grid in the survey area (Fig. 2). The station location within each grid was initially chosen randomly, but once determined, the same location has been fished each year. The abundance of crab within each grid was estimated from the survey catch rates by block kriging. Two estimates were obtained for each grid in each year: the abundance of adult male crab with CW ≥95 mm, either including (N_1) or excluding soft-shelled crab (N_2). $N_{1,i}$ is an estimate of the number of crabs that will be available to the fishery in grid i in the following year. $N_{2,i}$ is

© 2003 NRC Canada

Fig. 1. Fishing zones for snow crab (*Chionoecetes opilio*) in the southern Gulf of St. Lawrence.

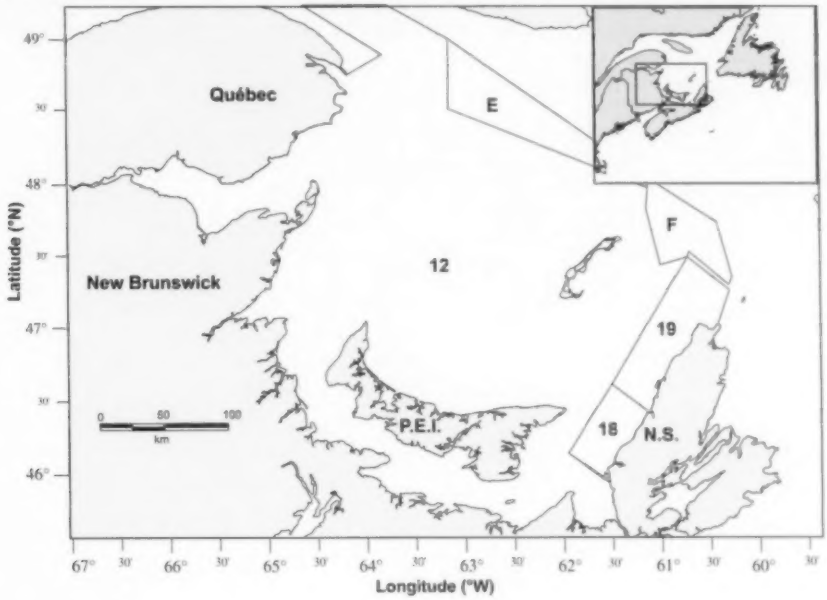
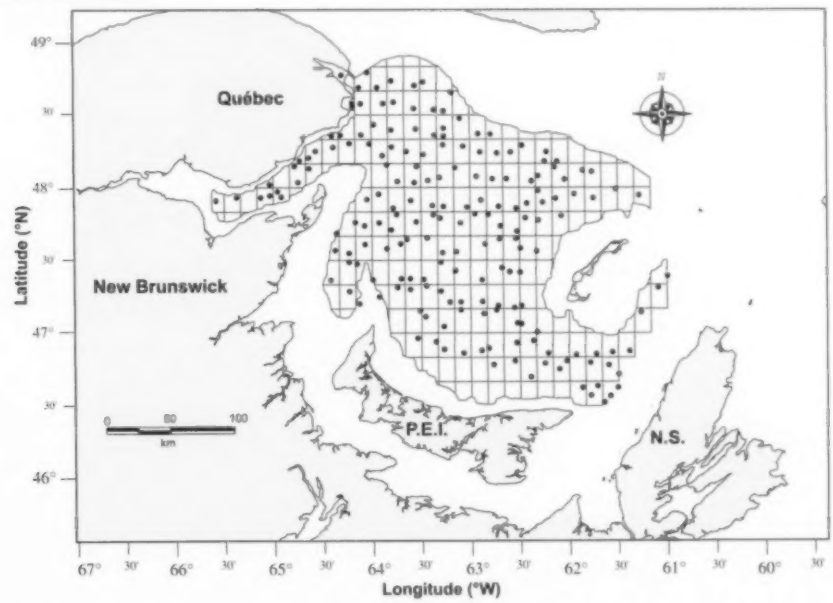


Fig. 2. Annual research survey for snow crab (*Chionoecetes opilio*) in the southern Gulf of St. Lawrence, showing 10-min grids and the distribution of sampling locations.



an estimate of the number of exploitable crabs that survived the fishery in grid i in the survey year.

Analyses

We compared the distribution of fishing effort and fishery catch rates (CPUE, kg·trap^{-1}) among grids with estimates of crab abundance in each grid. Only grids in which there was fishing activity in a particular year were included in the analysis. We used $N_{1,i,t-1}$, the estimated abundance of commercial-sized adult males crabs (both hard- and soft-shelled) in grid i, based on the survey in year $t - 1$, to predict crab distribution at the beginning of the fishery in year t. The average crab abundance in grid i during the fishery in year t was estimated as

$$(1)\quad N_{AV_{i,t}} = (N_{1,i,t-1} + N_{2,i,t}) / 2$$

© 2003 NRC Canada

Assumptions underlying these comparisons are that natural mortality is negligible (or at least spatially uniform) between the survey in year $t - 1$ and the fishery in year t and that commercial-sized adult male crabs move little between the survey and the subsequent fishery. In tagging experiments conducted on adult male crabs in zone 12 in the 1960s, most individuals were recovered within 15 miles of their release site (Watson 1970; Watson and Wells 1972). Similarly, in experiments conducted in the 1980s, most crabs recovered within 2 years of release were captured within 15 km of their release site (Lefebvre and Brêthes 1991). To verify whether the postfishery survey in year $t - 1$ provided a reasonable prediction of crab distribution at the start of the fishery in year t, we compared $N_{1,i,t-1}$ with $N_{3,i,t}$, an estimate of crab abundance in grid i based on data from the fishery and survey in year t:

$$(2) \qquad N_{3,i,t} = C_{i,t} + N_{2,i,t}$$

where $C_{i,t}$ is an estimate of the number of crabs removed from grid i by the fishery in year t. We estimated $C_{i,t}$ by multiplying the catch (kg) from grid i by the average number of commercial-sized adult male crabs per kg in year t.

An alternate estimate of the average crab abundance in grid i during the fishery in year t would be one-half of the fishery catch from grid i plus the survey estimate of the number of exploitable crabs that survived the fishery in grid i (i.e., 50% of $C_{i,t}$ plus $N_{2,i,t}$). Unlike N_{AV}, this estimate would not be subject to error because of natural mortality and the movement of crabs between the survey in year $t - 1$ and the fishery in year t. The difficulty with this estimate is that it is not independent of fishing effort (because fishery catch is a function of effort). This will result in spurious positive correlations between effort in a grid and estimated crab abundance in the grid. As expected from this lack of independence, correlations between effort and this alternate estimate of crab abundance were on average over 50% stronger than the correlations between effort and N_{AV} (although correlations with CPUE were similar using either estimate of abundance). Thus, results reported below are restricted to analyses using N_{AV}, an estimate of local crab abundance based entirely on survey data and independent of fishery catch and effort.

A potential difficulty with our analyses is that fishery data are in weight, whereas survey estimates of crab distribution are available only in numbers. Thus, a lack of correspondence between the spatial distribution of fishery catch rates and the spatial distribution of crabs based on the survey might reflect spatial variation in the average weight of commercial-sized crabs rather than effects of competition in the fishery. Fortunately, abundance of commercial-sized male crabs appears to predict their biomass well: the biomass of commercial-sized adult male crabs in survey tows is closely correlated with their abundance ($R^2 = 0.99$; E. Wade, unpublished data).

We compared fishery effort, fishery CPUE, and estimates of local crab abundance using two approaches. First, we calculated the Pearson's correlation coefficients between variables for each year. Variables were $\log_e$ transformed for this analysis. Because these variables are spatially autocorrelated, we assessed the significance of these correlations based on the effective sample size, taking the spatial structure of the variables into account. Computations followed Dutilleul (1993) and were made using a modification of the fortran program Mod_t_test (Legendre 2000).

Second, we tested for significant differences between spatial distributions using the test described by Syrjala (1996). To conduct this test, each variable was first normalized by dividing each observation by the sum over all locations for that variable. For each sampling location k, a cumulative distribution function for variable i can be defined as

$$(3) \qquad \Gamma_i(x_k, y_k) = \sum_{\forall x \le x_k, \forall y \le y_k} \gamma_i(x, y)$$

where γ_i is normalized variable i, and x and y give the grid position along the longitudinal and latitudinal axes. The test statistic was the square of the difference between these cumulative distribution functions for the two variables being compared, summed over all K grids:

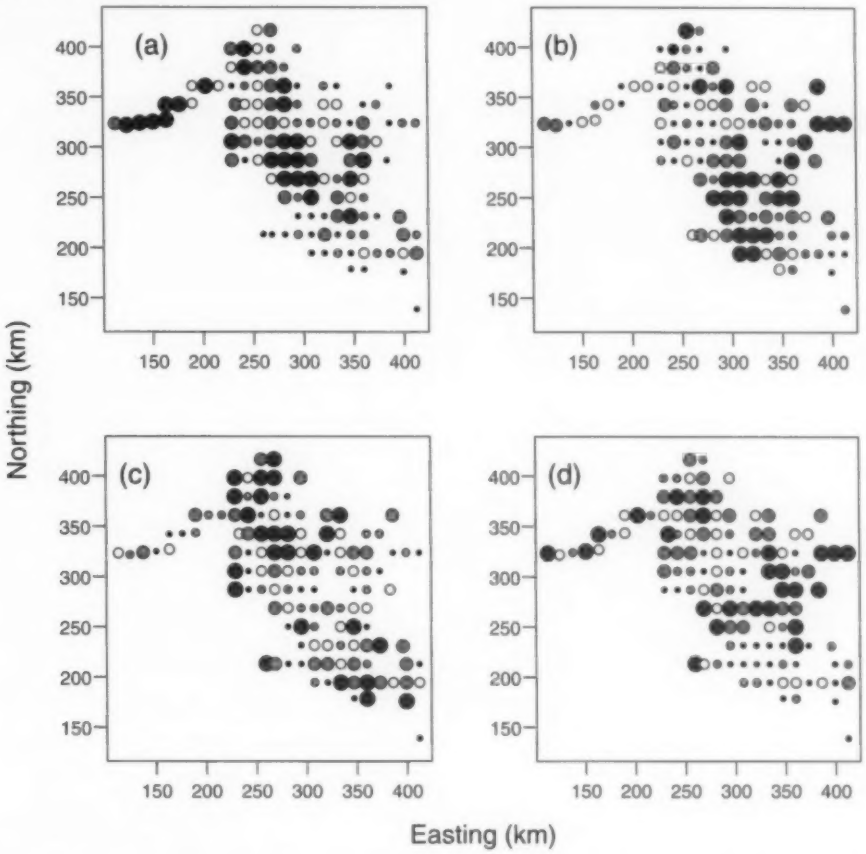
$$(4) \qquad \psi = \sum_{k=1}^{K} [\Gamma_1(x_k, y_k) - \Gamma_2(x_k, y_k)]^2$$

Because the statistic ψ depends on the corner of the grid system used as the origin, it was calculated starting at each of the four corners, and the average of the four values was used as the test statistic. Significance was determined using a randomization test. Under the null hypothesis that the spatial distributions of the two variables are the same, either observation $\gamma_i(x_k, y_k)$ is equally likely for each of the two variables. A random permutation of the data was constructed by randomly assigning one of the two values at each location to one of the variables and the other value to the second variable. This procedure was repeated 999 times, and the significance level was given by the proportion of the 1000 permutations (including the observed permutation) with a test statistic as great or greater than that obtained from the observed data.

Departures from the spatial allocation of effort predicted by the IFD could result from travel costs. To test this, we conducted multiple linear regression analyses relating the effort in a grid to the exploitable crab abundance in that grid and its distance from port. Distance was the average distance from home port for each trip to a particular grid in a particular year, weighted by the effort for that trip. Effort and crab abundance were $\log_e$ transformed for this analysis. Statistical significance was assessed in two ways. First, each independent variable was correlated with the residuals from a regression model that included only the other independent variable. Significance of these correlations was calculated based on the effective sample size given the spatial structure of the residuals and the independent variable, as described above. Second, significance was calculated based on random simulations of the dependent variable, $\log_e$-transformed effort. Spatial structure was estimated for $\log_e$-transformed effort in each year using a spherical model. Gaussian random fields with the same spatial structure were generated using the grf function of the R package geoR (http://www.r-project.org/ and http://www.maths.lancs.ac.uk/~ribeiro/geoR/). An example of the observed data and random simulations with the same spatial structure is given in Fig. 3. Multiple linear regressions were computed using the simulated data as the dependent variable, and the t statistic for each of the independent variables was recorded. This procedure was repeated 999 times for each year, and significance of each of

© 2003 NRC Canada

Fig. 3. Observed distribution of $\log_e$(effort) and three random simulations with the same spatial structure. Circle size and shading indicate data quintile. Larger sizes indicate higher values.



the independent variables was calculated as $(N + 1)/1000$, where N is the number of random simulations giving a t value as extreme as that given by the observed data. For one-sided tests, only simulations giving a t value greater than that observed for crab abundance (where the expected direction of the effect is positive) or less than that observed for distance (where the expected direction is negative) contributed to N. The same two approaches were used to assess significance in multiple regressions relating exploitable crab abundance in a grid to fishery effort and catch rates in the grid.

We used Lorenz curves (Dagum 1985) to compare how evenly crab abundance, effort, and CPUE were distributed among grids. To construct these curves for, say, effort, we sorted grids by effort and plotted cumulative proportion of grids along the abscissa and cumulative proportion of effort along the ordinate. If effort were evenly distributed among grids, the Lorenz curve would be the identity function. As the distribution of effort becomes more unequal, the Lorenz curve becomes more concave.

Results

In all years, CPUE was more evenly distributed among grids than either effort or crab abundance (Fig. 4), consistent with the IFD prediction that it should tend to be equalized among areas. Though less evenly distributed than CPUE, crab abundance was more evenly distributed among grids than effort. This may be an artifact of the way in which crab abundance was estimated. Crab abundance in each grid was estimated by kriging, which will result in a smoothed distribution of abundance estimates.

The distribution of legal-sized crabs estimated from the postfishery survey in year $t - 1$ ($N_{1,i,t-1}$) was positively correlated with the distribution estimated from fishery catch and the postfishery survey in year t ($N_{3,i,t}$). Correlations were highly significant in all years (Table 1). Correlations were between 0.5 and 0.6 in the earliest and latest years in the time series (1990, 1991, 2000, 2001) but up to 0.8–0.9 in the intervening years. These correlations not only indicate that the survey in one year provides information about crab distribution the next year, but also indicate a level of uncertainty in these distributions. They suggest an upper limit in the range of 0.6–0.8 to the correlations expected between estimated crab distribution and fishery effort and CPUE even when effort and CPUE map true crab distribution well.

Effort in a grid was positively correlated with the estimated abundance of exploitable crabs in all years (Table 2). Correlations varied between about 0.4 and 0.5, except in 1993 when the correlation was less than 0.3. These correla-

© 2003 NRC Canada

Fig. 4. Lorenz curves for effort (dashed–dotted line), catch-per-unit-effort (CPUE; solid line), and local crab (*Chionoecetes opilio*) abundance (broken line) in 1990–1995 and 1998–2001.

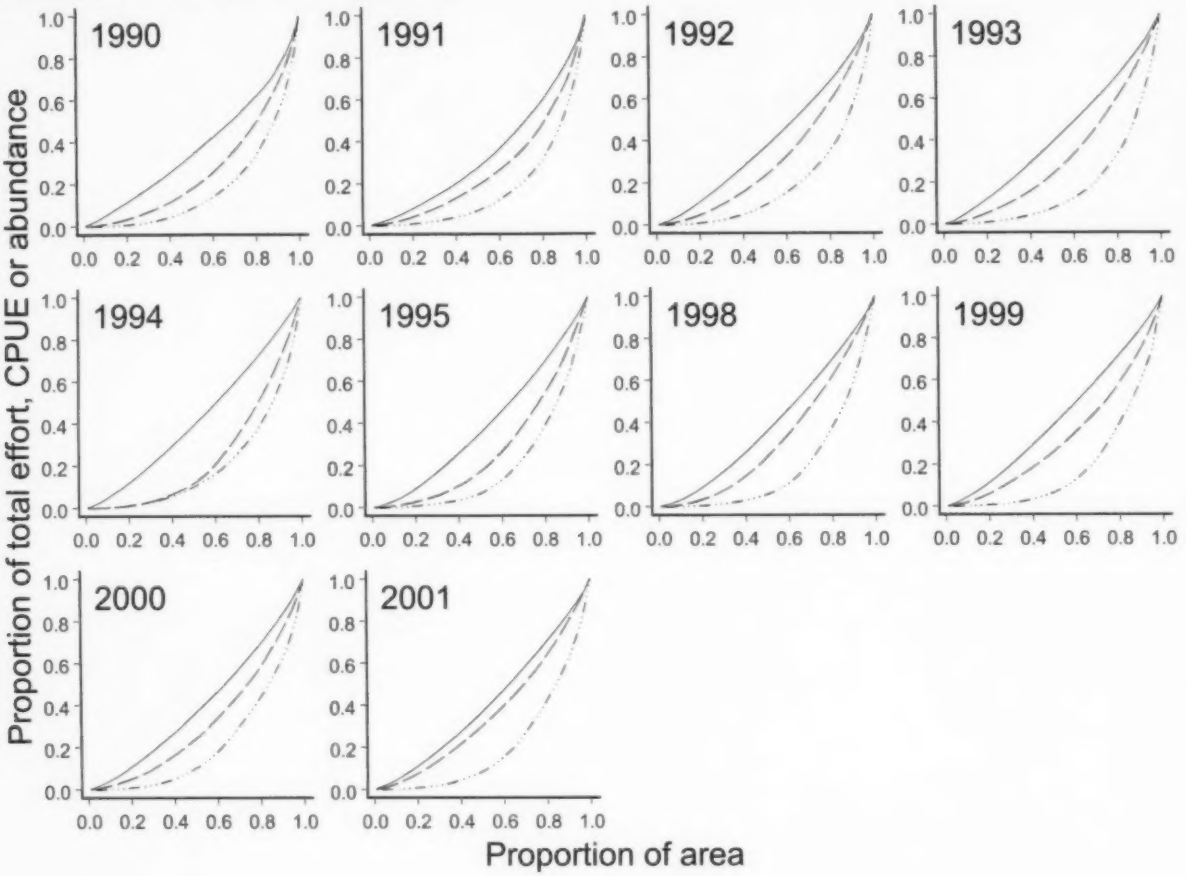


Table 1. Correlations (R) between $N_{1,i,t-1}$, crab distribution predicted from the postfishery survey in year $t-1$, and $N_{3,i,t}$, crab distribution estimated from landings in year t and the postfishery survey in year t.

Year t	n	R	df	P
1990	123	0.581	42.5	<0.0001
1991	114	0.572	29.0	0.0008
1992	126	0.803	14.8	0.0001
1993	120	0.744	15.3	0.0006
1994	131	0.859	7.9	0.0016
1995	154	0.775	10.7	0.0022
1998	134	0.893	11.6	<0.0001
1999	120	0.724	26.8	<0.0001
2000	135	0.539	67.4	<0.0001
2001	132	0.561	35.0	0.0003

Note: n is sample size; df is the effective degrees of freedom after adjustment for spatial autocorrelation; and P is the significance level based on the adjusted degrees of freedom.

tions were highly significant in all years except 1993. CPUE was also positively correlated with crab abundance in the six years since 1994. The strength of the correlation with abundance was similar for effort and CPUE in these years. Correlations were more significant with effort than with CPUE in all six years, but this reflects the lower statistical power (lower df because of higher spatial autocorrelation) in the tests with CPUE. However, in contrast to effort, CPUE was unrelated to crab abundance in the four years prior to 1994. Correlations between CPUE and crab abundance were not even in the expected positive direction in the 1990–1992 period. In these years when CPUE and crab abundance were negatively correlated, there was also a significant negative correlation between CPUE and effort. CPUE and effort were uncorrelated in other years except 1995 and 2001, when significant positive correlations occurred. Relationships between effort, CPUE, and crab abundance did not show any strong departures from linearity on a log scale, except perhaps for a tendency for CPUE to vary little at medium to high effort levels in some years.

In the earlier years (e.g., 1991), estimated crab abundance was clearly better mapped by effort than by CPUE (Fig. 5). CPUE tended to be low in the central area where crab abundance and effort were both highest and was highest in areas where crab abundance and effort were both low. In later years, CPUE tended to be more evenly distributed than both

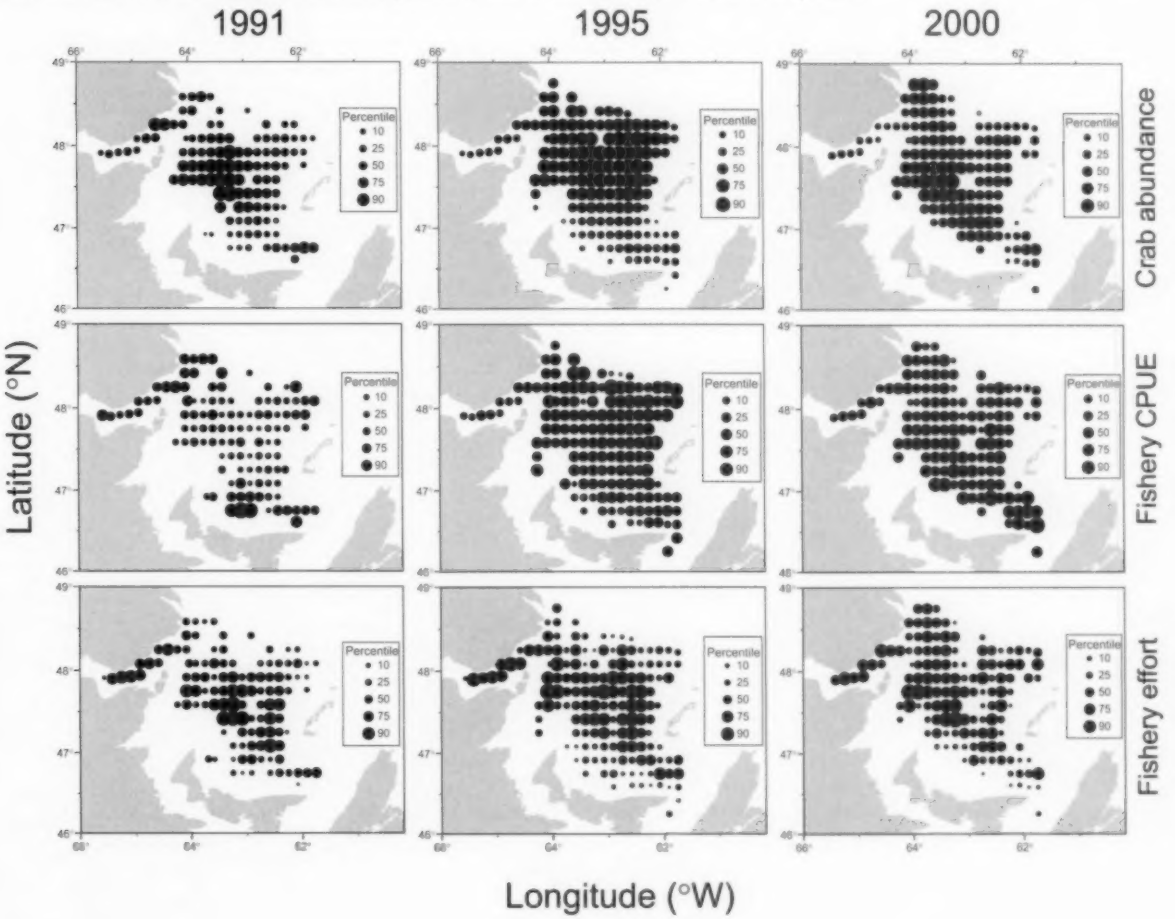
© 2003 NRC Canada

Table 2. Correlations (R) between the spatial distributions of crabs (N_{AV_i}), fishery effort (f_i), and fishery catch-per-unit-effort ($CPUE_i$).

		N_{AV_i} vs. f_i			N_{AV_i} vs. $CPUE_i$			$CPUE_i$ vs. f_i		
Year t	n	R	df	P	R	df	P	R	df	P
1990	123	0.477	44.3	0.0008	–0.104	40.2	0.509	–0.418	29.5	0.018
1991	114	0.521	24.9	0.0054	–0.281	26.1	0.147	–0.349	53.8	0.008
1992	126	0.466	33.8	0.0044	–0.181	89.0	0.086	–0.247	64.9	0.044
1993	120	0.276	33.6	0.1047	0.019	29.9	0.919	0.082	95.4	0.427
1994	132	0.417	33.0	0.0128	0.512	14.3	0.041	0.201	62.1	0.111
1995	154	0.503	32.0	0.0024	0.459	27.4	0.012	0.373	60.0	0.003
1998	134	0.534	29.0	0.0020	0.480	18.5	0.030	0.203	57.5	0.121
1999	120	0.369	57.7	0.0038	0.378	37.6	0.017	–0.085	84.4	0.435
2000	135	0.427	86.6	<0.0001	0.366	55.8	0.005	0.174	76.3	0.128
2001	132	0.374	70.2	0.0012	0.332	57.7	0.010	0.253	82.9	0.020

Note: N_{AV_i} is the estimated average abundance of recruited crabs in grid i during the fishery in year t; n is sample size; df is the effective degrees of freedom after adjustment for spatial autocorrelation; and P is the significance level based on the adjusted degrees of freedom.

Fig. 5. Spatial distributions of crab (*Chionoecetes opilio*) abundance, effort, and catch-per-unit-effort (CPUE) in the fishery in 1991, 1995, and 2000. The maximum value in each panel is scaled to the same symbol size in all panels.



crab abundance and fishery effort (e.g., see 1995 and 2000 in Fig. 5). Although it tended to be high in areas of high estimated crab abundance, it was also often relatively high in areas of low abundance and low effort. Discrepancies are also evident between the maps of effort and crab abundance in these later years. For example, estimated crab abundance tended to be high in the northeast corner of the grid system in 1995 (Fig. 5); effort in this area tended to be low in 1995

© 2003 NRC Canada

(and CPUE high). Similarly, effort was high in Chaleur Bay in all years, even when crab abundance in this area was estimated to be relatively low.

In 1990 and 1991, spatial distributions did not differ significantly between commercial-sized crabs and fishery effort, but highly significant differences occurred between the spatial distributions of crabs and CPUE (Table 3). In other years (except 1998 in the case of effort), significant differences in spatial distribution occurred between crab abundance and both fishery effort and CPUE, but these differences tended to be more significant for CPUE than for effort (Table 3). Even though differences were more significant for CPUE than for effort in most years, the test statistic ψ tended to be greater for effort than for CPUE. However, this statistic depends on the statistical distribution of the variables and is not directly comparable between the tests with effort and those with CPUE. To illustrate this, we compared the observed spatial distribution of effort with random permutations of effort and CPUE in each year. In each year, the average statistic over 1000 random permutations was greater using randomized effort than using randomized CPUE, even though the comparisons were with observed effort. The greater values of ψ in comparisons with effort than in those with CPUE appear to reflect differences in the statistical properties of the two variables (e.g., greater evenness in the distribution of CPUE).

Effort tended to be higher than expected from local crab abundance in Chaleur Bay and lower than expected north of P.E.I. (Fig. 6). Average distance to port was low for fishing trips in Chaleur Bay and high for trips north of P.E.I. (Fig. 6). We tested for an effect of distance-to-port on effort using multiple linear regressions with $\log_e$-transformed effort as the dependent variable and $\log_e$-transformed crab abundance and distance-to-port as the independent variables. In all years, effects of local crab abundance were positive, and distance-to-port negative (Table 4). After accounting for spatial structure, the effect of crab abundance was significant ($P < 0.05$) in most years based on either the adjusted degrees of freedom or random simulations (8 or 9 of the 10 years, respectively). On the other hand, the effect of distance was significant in none of the 10 years based on the adjusted degrees of freedom and in only 1 year based on random simulations (or in 2 years for one-sided tests). This lack of significance may reflect the low power of these tests after accounting for spatial structure. Distance-to-port exhibited an extremely strong spatial structure (Fig. 6), and effective sample size was low in the years with the strongest effects (Table 4). The probability of obtaining negative slopes in 10 out of 10 years is low if the true slope is zero. We combined the probabilities from the 10 individual analyses following Sokal and Rohlf (1981, p.780). This yielded two-sided significance levels for the effect of distance of 0.026 and 0.034, based on adjusted degrees of freedom and random simulations, respectively. Overall one-sided significance levels were 0.00044 and 0.00086, respectively.

We examined whether prediction of the spatial distribution of crabs could be improved by including both fishery effort and CPUE in the model. In 1990 and 1991, correlations between effort and estimated local crab abundance were nearly as strong as the correlations between the estimates of abundance based on the survey in one year and those based on fishery landings and the survey in the following year (Table 5). In these years, adding CPUE to the model accounted for negligible additional spatial variation in crab abundance. In 1994–2001, models including both fishery variables accounted for more of the spatial variation in crab abundance than did models including only one of the two variables, especially in the later years (Table 5). However, except in 2000, the amount of spatial variance in crab abundance accounted for by the fishery variables was substantially less than the spatial covariance between the two estimates of crab distribution. Significance levels were similar between the method based on adjusted degrees of freedom and that based on random simulations (Table 6). In all years except 1993, the model that included CPUE was significantly improved by the addition of effort. Controlling for the effect of effort, the effect of CPUE was significant in only 1998–2001 based on the adjusted degrees of freedom, or in 1994–1999 according to the random simulations in the case of two-sided tests, or in 1994–2001 according to both methods in the case of one-sided tests (Table 6). However, in the 1994–2001 period, the lower significance levels for CPUE than for effort are partly due to lower power. The average t value during this period was similar for the two variables (5.3 for effort and 4.8 for CPUE), but adjusted degrees of freedom were lower for the tests of CPUE than for the tests of effort (Table 6).

Table 3. Randomization tests for a difference in spatial distribution between commercial-sized snow crabs (N_{AV}) and either fishery effort (f) or fishery catch rate (catch per unit effort, CPUE).

	N_{AV} vs. f		N_{AV} vs. CPUE	
Year	ψ	P	ψ	P
1990	0.43	0.141	2.88	0.001
1991	0.28	0.115	1.26	0.001
1992	1.03	0.011	0.72	0.001
1993	0.83	0.032	0.58	0.001
1994	1.56	0.001	1.02	0.001
1995	0.88	0.001	0.63	0.001
1998	0.31	0.062	0.30	0.001
1999	0.46	0.013	0.35	0.001
2000	0.61	0.003	0.41	0.001
2001	0.42	0.025	0.18	0.001

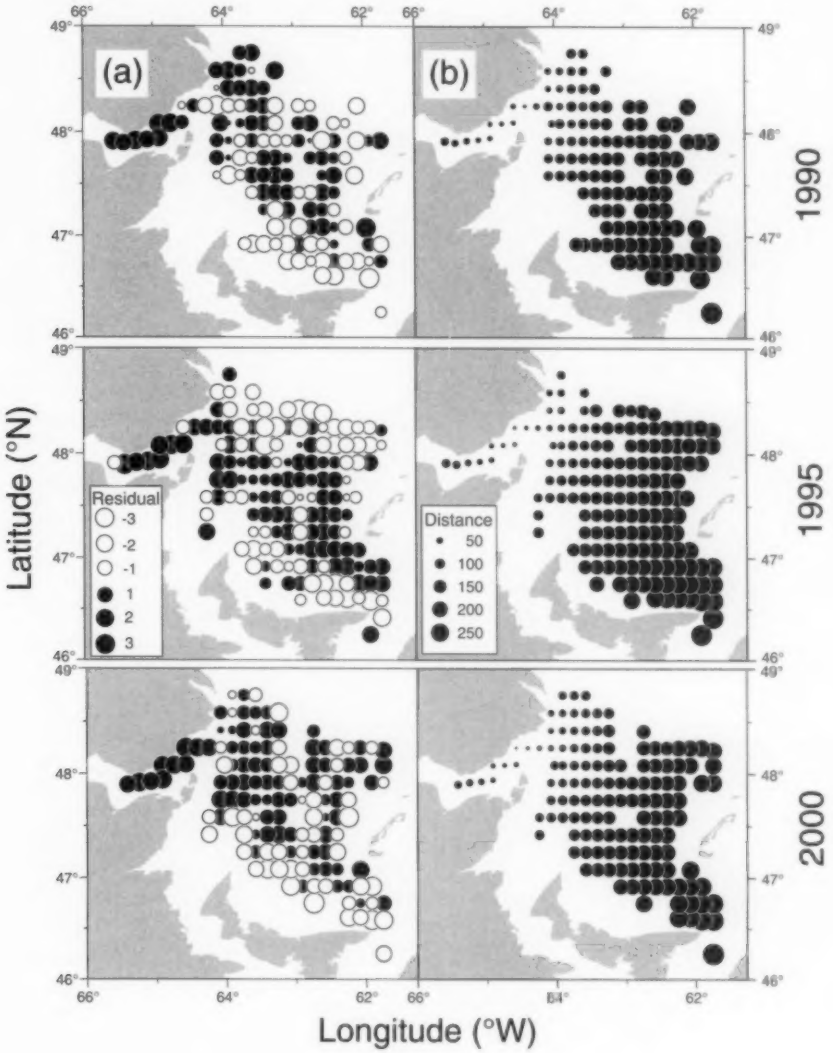
Note: ψ is the test statistic and P is its significance based on 1000 random permutations of the data under the null hypothesis of no difference in distribution.

Discussion

The purpose of this study was to test the IFD prediction that fishery effort should map resource distribution better than fishery catch rates. The result differed between time periods. In the early 1990s, the prediction was clearly correct: effort showed a significant positive relationship with local crab abundance but relationships between CPUE and crab abundance were weak and nonsignificant. During this period, the impression of resource distribution given by CPUE was completely misleading: CPUE was highest in areas of low crab abundance (and low effort) and low in areas of high abundance (and high effort). However, differences in the performance of effort and CPUE as indicators of resource dis-

© 2003 NRC Canada

Fig. 6. Residuals from $\log_e$(effort) predicted from (*a*) $\log_e$(local crab abundance) and (*b*) average distance (km) from port for 1990, 1995, and 2000.



tribution were less obvious in years since the mid-1990s. During this later period, both showed similar positive correlations with local crab abundance. Thus, effort and CPUE mapped resource distribution equally well in some years, but effort was the more consistent indicator of resource distribution, also performing well in years in which CPUE was misleading as an indicator of crab distribution.

Even though effort was the more consistent indicator of local crab density, significant discrepancies occurred between the maps of effort and crab abundance in most years. This is not surprising given the expected violations of the assumptions of the IFD. First, fishers are not free to move between areas without costs. Effort might be expected to be higher than predicted from resource abundance on fishing grounds close to port where travel costs are low and lower than predicted on distant grounds where travel costs are high. This tended to be the case in the crab fishery. Fishery regulations also limited access to some grids in some years. Beginning in 1997, grids with a high percentage of soft-shelled crabs in trap catches were identified each week. The frequency of soft-shelled crabs tended to increase as the fishing season progressed. In 1997–1999, soft-shelled crabs were a problem only late in the season when most of the fishing effort (>90%) had already been expended. In these years, 10–12% of the grids had high frequencies of soft-shelled crabs by the end of the fishing season, and fishers were asked, but not obligated, to avoid these areas. Soft-shelled crabs posed a greater problem in 2000 and 2001, and areas with a high frequency of soft-shelled crabs were closed to fishing in these years; about 15% of the grids were closed to fishing by midseason, when 65–75% of the effort had been expended, and 50–80% of the grids were closed by

© 2003 NRC Canada

Table 4. Predicting the spatial distribution of fishing effort from crab distribution ($\log_e N_{AV}$) and the distance of fishing grounds from port.

Year	n	b	t	$P2_{sim}$	$P1_{sim}$	r	df	P_{adj}
Predictor 1: $\log_e N_{AV}$								
1990	123	0.547	4.25	0.024	0.017	0.335	48.4	0.0169
1991	114	0.814	5.99	0.004	0.002	0.482	23.6	0.0135
1992	126	0.683	5.70	0.013	0.005	0.454	28.4	0.0110
1993	120	0.435	3.09	0.204	0.112	0.273	31.0	0.1239
1994	132	0.619	4.66	0.035	0.015	0.351	28.2	0.0562
1995	154	0.791	6.24	0.019	0.012	0.433	31.1	0.0117
1998	134	0.801	5.76	0.006	0.004	0.419	29.3	0.0184
1999	120	0.258	1.75	0.020	0.010	0.360	59.2	0.0043
2000	135	0.633	5.24	0.002	0.001	0.411	61.4	0.0008
2001	132	0.664	4.99	0.001	0.001	0.402	53.6	0.0022
Predictor 2: Distance								
1990	123	–0.601	–4.66	0.222	0.107	–0.363	17.6	0.1202
1991	114	–0.199	–1.47	0.576	0.295	–0.134	71.1	0.2566
1992	126	–0.417	–3.48	0.161	0.088	–0.298	29.6	0.0999
1993	120	–0.007	–0.05	0.989	0.494	–0.005	65.8	0.9701
1994	132	–0.053	–0.40	0.857	0.400	–0.033	101.3	0.7432
1995	154	–0.316	–2.50	0.429	0.208	–0.190	43.2	0.2092
1998	134	–0.489	–3.52	0.124	0.066	–0.274	32.2	0.1156
1999	120	–0.627	–4.22	0.167	0.093	–0.369	19.8	0.0929
2000	135	–0.606	–5.01	0.006	0.004	–0.397	16.1	0.1019
2001	132	–0.479	–3.60	0.075	0.039	–0.302	33.1	0.0776

Note: n is sample size; b is the standard partial regression coefficient for local crab abundance or distance to fishing grounds; t is b divided by its standard error; $P2_{sim}$ and $P1_{sim}$ are two- and one-sided significance levels, respectively, for t based on 1000 random simulations with the same spatial autocorrelation as log(fishing effort); r gives the correlation between one of the predictors and the residuals from the linear regression using the other predictor; df is the effective degrees of freedom adjusting for spatial autocorrelation of the residuals and the predictor; and P_{adj} is the significance level for r based on df.

Table 5. Proportion (r^2) of the spatial variation in crab abundance ($\log_e N_{AV}$) accounted for by spatial variation in fishery effort ($\log_e f$) and catch per unit effort (CPUE; $\log_e$CPUE).

Year t	Effort	CPUE	Both	$N_{1,t-1}$ vs. $N_{3,t}$
1990	0.23	0.01	0.24	0.34
1991	0.27	0.08	0.28	0.33
1992	0.22	0.03	0.22	0.64
1993	0.08	0.00	0.08	0.55
1994	0.17	0.26	0.36	0.74
1995	0.25	0.21	0.34	0.60
1998	0.29	0.23	0.43	0.80
1999	0.14	0.14	0.30	0.52
2000	0.18	0.13	0.27	0.29
2001	0.14	0.11	0.20	0.31

Note: Correlations (r^2) between the crab distributions estimated from the survey in year $t - 1$ ($N_{1,t-1}$) and from the fishery and survey in year t ($N_{3,t}$) are included for comparison.

the end of the season. Thus, area closures may have constrained the correspondence between the distributions of effort and crab abundance in 2000 and 2001, though this is not evident from the relatively strong correlations between the two variables in these years.

Second, knowledge of the distribution of resources, fishing effort, and fishing success is less than ideal in any fishery. This is likely to be especially true in a competitive fishery when the exchange of information between fishers may be limited. Though fishers in the zone 12 crab fishery have received individual quotas since 1990, all fishers competed for the same overall quota in earlier years. A carryover of competitive behaviour into the first years of the noncompetitive fishery in the early 1990s may have contributed to departures from the IFD prediction of equalized catch rates among areas in these years.

Third, fishers are expected to vary in competitive ability. In the snow crab fishery, fishers varied in the size of their vessels, in the number of traps with which they were allowed to fish, and in their experience in the fishery. In 1995–1997, 2000, and 2001, a portion of the quota (10–30%) was allocated to temporary license holders. These temporary fishers were active later in the season than the permanent fishers and tended to be less likely to move their traps in search of better catch rates. Variation in the competitive ability of fishers is expected to result in the overuse of areas of below-average resource abundance and the underuse of areas of above-average abundance (Abrahams and Healey 1990).

Measurement error, and mortality and movement of crabs between the survey in one year and the fishery in the next year, also contribute to the discrepancies between the maps of effort or CPUE and crab abundance. However, in all years, the correspondence between crab distribution estimated from the survey in one year and the distribution estimated from the fishery and survey in the following year was greater (in most years, much greater) than the correspondence between the distributions of effort or CPUE and crab abundance. This indicates that these factors were not the principle cause of the discrepancies between the distributions of effort or CPUE and estimated crab abundance. Errors in the measures of effort and CPUE may also contribute to these discrepancies. One source of error is variation in

© 2003 NRC Canada

Table 6. Predicting the spatial distribution of crabs ($\log_e N_{AV}$) from fishery effort ($\log_e f$) and catch-per-unit-effort (CPUE; $\log_e$CPUE).

Year	n	b	t	$P2_{sim}$	$P1_{sim}$	r	df	P_{adj}
Predictor 1: $\log_e f$								
1990	123	0.566	5.99	0.002	0.002	0.436	49.7	0.0013
1991	114	0.450	5.61	0.001	0.001	0.441	31.1	0.0101
1992	126	0.378	5.46	0.007	0.004	0.428	35.4	0.0079
1993	120	0.235	3.10	0.114	0.051	0.275	33.7	0.1063
1994	132	0.532	4.57	0.015	0.010	0.365	38.1	0.0203
1995	154	0.437	5.40	0.008	0.007	0.373	39.4	0.0157
1998	134	0.500	6.75	0.008	0.004	0.497	38.1	0.0011
1999	120	0.298	5.22	0.005	0.004	0.433	55.9	0.0007
2000	135	0.303	4.97	0.028	0.012	0.391	83.0	0.0002
2001	132	0.188	4.99	0.014	0.006	0.307	85.0	0.0038
Predictor 2: $\log_e$CPUE								
1990	123	0.124	1.31	0.580	0.270	0.108	63.7	0.3891
1991	114	–0.105	–1.31	0.513	0.747	–0.116	33.5	0.5050
1992	126	–0.059	–0.85	0.748	0.596	–0.074	87.0	0.4888
1993	120	–0.003	–0.04	0.990	0.492	–0.004	26.8	0.9844
1994	132	0.725	6.22	0.022	0.012	0.471	15.2	0.0550
1995	154	0.358	4.42	0.034	0.022	0.314	30.6	0.0771
1998	134	0.426	5.75	0.002	0.001	0.439	21.2	0.0350
1999	120	0.304	5.33	0.003	0.001	0.440	37.2	0.0049
2000	135	0.243	3.99	0.059	0.027	0.323	53.9	0.0154
2001	132	0.154	3.11	0.073	0.037	0.256	58.1	0.0484

Note: n is sample size; b is the standard partial regression coefficient for $\log_e f$ or $\log_e$CPUE; t is b divided by its standard error; $P2_{sim}$ and $P1_{sim}$ are two- and one-sided significance levels, respectively, for t based on 1000 random simulations with the same spatial autocorrelation as $\log_e N_{AV}$; r is the correlation between one of the predictors and the residuals from the linear regression using the other predictor; df is the effective degrees of freedom adjusting for spatial autocorrelation of the residuals and the predictor; and P_{adj} is the significance level for r based on df.

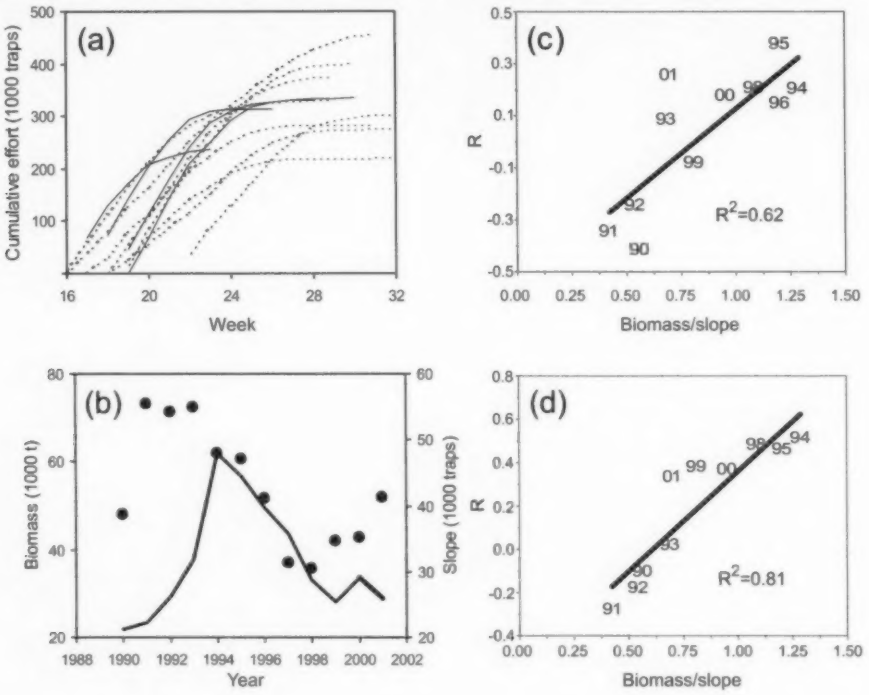
soak time, the elapsed time between setting and hauling a trap. No adjustments for variation in soak time were made in our analyses. The relationship between crab catch and soak time is expected to be asymptotic as a result of gear saturation at long soak times (Miller 1990). Soak time in the zone 12 fishery generally appears to be long enough for gear saturation to occur, so that CPUE is independent of soak time in most years (Hébert et al. 2000). Because there is generally no relationship between CPUE and soak time in this fishery, no adjustments for soak time are made in assessments of this stock (Hébert et al. 2002*b*). Thus, variation in soak time does not appear to be an important source of discrepancies between maps of crab abundance and fishery effort or CPUE. In particular, it cannot account for the failure of CPUE to map crab abundance in the early 1990s because there was no relationship between CPUE and soak time in those years (Hébert et al. 2000).

Interference competition appears to occur in the crab fishery. CPUE tended to be equalized between areas compared with the distributions of local crab abundance and fishery effort. This is evident in both the Lorenz curves and the distribution maps. Interference appeared to be extreme in the early 1990s. During this period, there was a significant inverse relationship between CPUE and effort, indicating that fishing behaviour was far from that of "ideal-free" foragers. A number of factors may have contributed to increased competition during this period. First, crab abundance was at a low level (Fig. 7*b*), so that fishers had to compete for a smaller resource. Second, during the competitive fishery in years before 1990, there was an incentive to catch as much crab as possible, as quickly as possible. This may have resulted in a more intense fishery, and this behaviour may have continued for a number of years after the introduction of individual quotas in 1990. Plots of cumulative weekly effort suggest that the fishery was indeed prosecuted more quickly in the early 1990s than in later years (Fig. 7*a*). Slopes of these curves were exceptionally high in 1991–1993, indicating a particularly intense fishery in these years (Fig. 7*b*). We constructed an index of fishing intensity by dividing crab biomass by the slope of the cumulative effort curve (low values of the index indicate high fishing intensity). The correlations between CPUE and effort and between CPUE and local crab abundance were closely related to this index of fishing intensity (Figs. 7*c*, 7*d*). Both correlations were negative when fishing intensity was high (i.e., low values of the index) and positive when it was low. This suggests that spatial patterns in CPUE provide a misleading picture of resource distribution when fishing intensity is high but may be a useful indicator of resource distribution when fishing intensity and, thus, competition are lower. In the first years after the introduction of individual quotas, when crab biomass was low, effort appeared to be concentrated in areas of relatively high crab biomass, with the overuse of these areas resulting in low CPUE despite high local biomass. The better correspondence between CPUE and crab distribution in later years when fishing intensity was lower could reflect either a lack of competition in the fishery or the predicted underuse of high-biomass areas when fishers differ in competitive ability. The tendency for CPUE to be equalized among areas suggests that the explanation involves the underuse of high-quality areas rather than the absence of competition in the fishery.

Beginning in the mid-1990s, prediction of local crab abundance was substantially improved by including both ef-

© 2003 NRC Canada

Fig. 7. Relationships between fishing intensity and the correlation of catch-per-unit-effort (CPUE) with effort and local crab (*Chionoecetes opilio*) abundance. (*a*) Cumulative weekly effort in the 1990–2001 fisheries; solid lines, 1990–1993; broken lines, 1994–2001. (*b*) Slopes of the cumulative weekly effort curves between the 10th and 95th percentiles (circles) and estimated exploitable crab biomass in zone 12 (line). (*c*) The spatial correlation between CPUE and effort (R) versus an index of fishing intensity, crab biomass divided by the cumulative effort slope (low values of the index correspond to high fishing intensity). Numbers denote fishery year. (*d*) The spatial correlation between CPUE and local crab abundance (R) versus the index of fishing intensity.



fort and CPUE in models. This could reflect high CPUE in underused areas and low CPUE in overused areas. This suggests the use of a composite index of fishery data to map resource abundance. A composite index can be constructed by adding standardized effort to standardized CPUE (where the standardized variables are calculated by subtracting the mean and dividing by the standard deviation). In our case, this composite index explained 1.5–2.0 times as much of the spatial variation in crab abundance as either effort or CPUE alone in the 1994–2001 period. However, the difficulty with this approach is that CPUE was not consistently related to local crab abundance. Thus, including it in models as a predictor of crab abundance would produce more distorted rather than better maps of crab distribution in some years. For example, in the 1990–1992 period, the composite index accounted for much less of the spatial variation in crab abundance than effort alone (R^2 = 0.04–0.12 for the composite index and 0.22–0.27 for effort alone). These were also the years in which CPUE was negatively related to effort, and this could have been used as a flag to exclude CPUE from models in our case.

In conclusion, fishery data need to be used with caution when attempting to map resource distribution. The IFD predicts that effort should be a better indicator of resource distribution than CPUE when interference occurs in a fishery. In our case, the spatial distributions of effort and crab abundance were positively correlated in all years. CPUE was as closely related as effort to crab distribution in some years but was completely misleading in other years when fishing intensity and competition appeared to be high. Thus, effort was the more reliable indicator of resource distribution. However, even effort provided a distorted view of resource distribution. This distortion is expected given the likely violation of IFD assumptions.

Acknowledgements

We thank Darren M. Gillis and Martin Castonguay for helpful discussion of this work, Mikio Moriyasu and Marcel Hébert for helpful comments on an earlier version of the manuscript, and Christine Sabean and Jocelyn Denis for help with database preparation. Comments by two anonymous reviewers improved the manuscript.

References

Abrahams, M.V., and Healey, M.C. 1990. Variation in the competitive abilities of fishermen and its influence on the spatial distribution of the British Columbia salmon troll fleet. Can. J. Fish. Aquat. Sci. **47**: 1116–1121.

Abrahams, M.V., and Healey, M.C. 1993. Some consequences of variation in vessel density: a manipulative field experiment. Fish. Res. **15**: 315–322.

© 2003 NRC Canada

Conan, G.Y., and Comeau, M. 1986. Functional maturity of male snow crab (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. **43**: 1710–1719.

Dagum, C. 1985. Lorenz curve. *In* Encyclopedia of statistical sciences. *Edited by* S. Kotz and N.L. Johnson. John Wiley & Sons, New York. pp. 156–161.

Dutilleul, P. 1993. Modifying the *t* test for assesssing the correlation between two spatial processes. Biometrics, **49**: 305–314.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, N.J.

Fretwell, S.D., and Lucas, H.L. 1970. On territorial behaviour and other factors influencing the habitat distribution of birds. I. Theoretical development. Acta Biotheor. **19**: 16–36.

Garrod, D.J. 1964. Effective fishing effort and catchability coefficient. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, **155**: 66–70.

Gillis, D.M. 1999. Behavioral inferences from regulatory observer data: catch rate variation in the Scotian Shelf silver hake (*Merluccius bilinearis*) fishery. Can. J. Fish. Aquat. Sci. **56**: 288–296.

Gillis, D.M., and Peterman, R.M. 1998. Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. Can. J. Fish. Aquat. Sci. **55**: 37–46.

Gillis, D.M., Peterman, R.M., and Tyler, A.V. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. Can. J. Fish. Aquat. Sci. **50**: 323–333.

Gulland, J.A. 1964. The reliability of catch per unit effort as a measure of abundance in North Sea trawl fisheries. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, **155**: 99–102.

Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? Can. J. Fish. Aquat. Sci. **58**: 1760–1772.

Hébert, M., Hébert, A., Wade, E., Surette, T., Giard, P., DeGrâce, P., Biron, M., and Moriyasu, M. 2000. The 1999 assessment of snow crab, *Chionoecetes opilio*, stock in the southwestern Gulf of St. Lawrence (Areas 12–25/26, E and F). Canadian Stock Assessment Secretariat Res. Doc. 2000/014.

Hébert, M., Benhalima, K., Miron, G., and Moriyasu, M. 2002*a*. Moulting and growth of male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788) (Crustacea: Majidae), in the southern Gulf of St. Lawrence. Crustaceana, **75**: 671–702.

Hébert, M., Wade, E., Surette, T., and Moriyasu, M. 2002*b*. The 2001 assessment of snow crab, *Chionoecetes opilio*, stock in the southern Gulf of St. Lawrence (Areas 12, E and F). Canadian Stock Assessment Secretariat Res. Doc. 2002/013.

Lefebvre, L., and Brêthes, J.-C. 1991. Orientation des déplacements de crabes des neiges mâles (*Chionoecetes opilio*) marqués dans le sud-ouest du golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci. **48**: 1167–1175.

Legendre, P. 2000. Program Mod_t_test. Departement de sciences biologiques, Université de Montréal. Available at http://www.fas.umontreal.ca/BIOL/legendre/.

Miller, R.J. 1990. Effectiveness of crab and lobster traps. Can. J. Fish. Aquat. Sci. **47**: 1228–1251.

Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, **155**: 152–163.

Rose, G.A., and Leggett, W.C. 1991. Effects of biomass–range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **48**: 843–848.

Sainte-Marie, B., and Hazel, F. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **49**: 1282–1293.

Sainte-Marie, B., Raymond, S., and Brêthes, J.-C. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. **52**: 903–924.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. W.H. Freeman and Company, San Francisco, Calif.

Syrjala, S.E. 1996. A statistical test for a difference between the spatial distributions of two populations. Ecology, **77**: 75–80.

Vignaux, M. 1996. Analysis of vessel movements and strategies using commercial catch and effort data from the New Zealand hoki fishery. Can. J. Fish. Aquat. Sci. **53**: 2126–2136.

Watson, J. 1970. Tag recaptures and movements of adult male snow crabs *Chionoecetes opilio* (O. Fabricius) in the Gaspé region of the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rep. No. 204.

Watson, J., and Wells, P.G. 1972. Recaptures and movements of tagged snow crabs (*Chionoecetes opilio*) in 1970 from the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rep. No. 349.

© 2003 NRC Canada

Stress and saltwater-entry behavior of juvenile chinook salmon (*Oncorhynchus tshawytscha*): conflicts in physiological motivation

Carol Seals Price and Carl B. Schreck

Abstract: Two experiments were conducted to determine the effects of a mild or severe stressor on the saltwater preference of juvenile spring chinook salmon (*Oncorhynchus tshawytscha*). To observe the response of fish to an overhead threat, we presented stressed fish with an avian predator model in the second experiment. Experiments were conducted in 757-L tanks containing a stable vertical salinity gradient. Only 69% of fish stressed by being chased for 2 min before saltwater introduction (mild stressor) held in salt water, whereas 95% of unchased control fish preferred the saltwater layer. After the more severe handling and confinement stressor, only 20% of fish entered and remained in salt water compared with 100% of unstressed controls. After the presentation of the avian model, stressed fish holding in fresh water moved into the saltwater layer, but this behavioral response was transient. Fish began returning to fresh water within 10 min, and after 1 h, only 26% of stressed fish remained in the saltwater layer. Stress significantly decreases the saltwater preference of chinook salmon that would otherwise select full-strength salt water and may affect behavior in the estuary. Although smoltification primes these fish for seawater residence, stress apparently induced a conflicting physiological motivation.

Résumé : Deux expériences ont servi à déterminer les effets de facteurs de stress, légers ou intenses, sur les préférences de salinité de l'eau chez de jeunes saumons quinnat (*Oncorhynchus tshawytscha*) du printemps. Dans la seconde expérience, des poissons stressés ont été mis en présence de modèles d'oiseaux prédateurs pour observer leur réaction à une menace venant d'en haut. Les expériences se sont déroulées dans des bassins de 757 L présentant un gradient vertical stable de salinité. Seulement 69 % des poissons stressés par une poursuite de 2 min avant leur introduction en eau salée (facteur de stress léger) restent en eau salée, alors que 95 % des poissons témoins non pourchassés préfèrent la couche d'eau salée. Après un stress plus important dû à la manipulation et au confinement, seulement 20 % des poissons pénètrent dans l'eau salée et y demeurent, alors que 100 % des poissons témoins non stressés restent en eau salée. Après la présentation du modèle aviaire, les poissons stressés qui se tiennent en eau douce se déplacent vers l'eau salée, mais cette réaction comportementale est transitoire. Les poissons commencent à retourner en eau douce en moins de 10 min et, au bout de 1 h, seulement 26 % des poissons stressés sont encore dans la couche d'eau salée. Le stress diminue de façon significative la préférence pour l'eau salée chez des saumons quinnat qui choisiraient, dans d'autres circonstances, de l'eau salée de pleine concentration et il peut ainsi affecter leur comportement dans l'estuaire. Alors que la transformation en saumoneaux prédispose ces poissons à la vie en eau salée, le stress semble induire une motivation physiologique contradictoire.

[Traduit par la Rédaction]

Introduction

Juvenile spring chinook salmon (*Oncorhynchus tshawytscha*) outmigrating through novel estuarine environments may be faced with an array of environmental stressors before entering seawater, but little is known about how stress might alter the behavior of these fish with respect to saltwater entry. The physiological characteristics of the stress response have been thoroughly studied in salmonids (Pickering 1981; Adams 1990; Iwama et al. 1997). However, behavioral assays of stress are less common. Many authors promote behavioral studies as a link between small-scale, individual physiological processes and large-scale, population processes (Schreck 1990; Wedemeyer et al. 1990; Schreck et al. 1997). Thus, investigating behavioral aberrations may lend insight into the ecological significance of stress for fishes.

Received 13 September 2002. Accepted 4 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 September 2003.
J17097

C.S. Price[1,2] and C.B. Schreck. Oregon Cooperative Fish and Wildlife Research Unit, Biological Resources Division, U.S. Geological Survey, Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331-3803, U.S.A.

[1]Corresponding author (carolseals@hotmail.com).
[2]Present address: 132 Conch Ct., Emerald Isle, NC 28594, U.S.A.

 doi: 10.1139/F03-080 © 2003 NRC Canada

Laboratory studies involving behavioral effects of stress often focus on interactions of stressed salmonids with predators. Kruzynski and Birtwell (1994) found that juvenile chinook salmon exposed to the antisapstain fungicide 2-(thiocyanomethylthio) benzothiazole (TCMTB) were five times more likely than unexposed fish to be eaten by yellowtail rockfish (*Sebastes flavidus*). Juvenile coho salmon (*Oncorhynchus kisutch*) subjected to a simple handling stressor and allowed a 1-min recovery period were more susceptible to predation by lingcod (*Ophiodon elongatus*) than unstressed controls (Olla et al. 1992). In that study, no difference in predation rate was evident if fish were allowed to recover for more than 90 min. Similarly, Mesa (1994) showed that stressed juvenile chinook salmon were preferentially preyed upon by northern pikeminnow (*Ptychocheilus oregonensis*), but after 1 h, stressed and unstressed fish were consumed equally. Studies by Järvi (1989*a*, 1989*b*) support the notion that stress also inhibits normal predator-avoidance behavior in Atlantic salmon (*Salmo salar*).

Additional studies have investigated behavioral deviations resulting from stress. Cover-seeking time was increased for juvenile chinook salmon exposed to multiple acute handling stressors (Sigismondi and Weber 1988). Pulp mill effluent altered the schooling behavior of chum (*Oncorhynchus keta*) and coho salmon (Birtwell and Kruzynski 1989). Feeding activity of salmonids decreases in response to several stressors including acidity (Jones et al. 1987), toxicants (Folmar et al. 1981; Jones and Hara 1988), and handling (Pickering et al. 1982; McCormick et al. 1998). Chinook salmon smolts suffering from advanced bacterial kidney disease (BKD) showed a decreased preference for salt water (Price and Schreck 2003) and an increased risk of predation (Mesa et al. 1999).

The physiological stress response is considered an adaptive mechanism by which a perturbed organism attempts to regain homeostasis and increase survival (Selye 1950; McEwen 1998; Schreck 2000). However, the above examples indicate that stress-induced behavioral changes may place fish at a higher risk of predation. In nature, fish are often exposed concomitantly to several conflicting stimuli or stressors and must make choices to maximize survival. Although the stress itself may not be lethal, "ecological death" may ensue when the synergistic effects of multiple stressors result in maladaptive behavior inappropriate within the fish's ecological context (Schreck et al. 1997).

We conducted two laboratory experiments to determine the effects of relatively mild stressors on the saltwater-entry behavior of yearling "ocean-type" spring chinook salmon smolts. Radiotracking studies indicate that spring chinook salmon outmigrate through the Columbia River with the current (C.B. Schreck, unpublished data). Thus estuarine residence time is very brief (several hours) compared with other life history types that may reside in the estuary for days or months. Because these fish must quickly make the transition into salt water, factors that decrease their preference for salt water may be detrimental to successful outmigration. We wanted to simulate stress levels experienced by fish naturally migrating through the estuary and encountering salt water for the first time. Additionally, we were interested in the combined effects of stress and an avian predator model on saltwater-entry behavior. Our results suggest that the conflicting physiological demands of stressed salmon encountering salt water can lead to suboptimal behavior, and we discuss possible ecological ramifications of this behavior.

Methods

Test fish

Yearling chinook salmon used in these experiments were obtained as fingerlings (5–10 cm) from Oregon's South Santiam (experiment I) and Marion Forks (experiment II) hatcheries and reared at Oregon State University's Fish Performance and Genetics Laboratory at Smith Farm, Corvallis, Oregon. Both hatcheries are within the Willamette River system and the stocks are genetically similar (Myers et al. 1998). Fish were held indoors with natural lighting in 2-m-diameter, circular tanks and fed to satiation twice per day for at least 4 months until needed for experiments. During rearing, water temperature was 12.8–14 °C. In experiment I, yearling chinook measured 16.9 ± 2.9 (± standard deviation) cm and weighed 59.6 ± 26.5 g. In experiment II, yearling chinook salmon measured 16.8 ± 2.2 cm and weighed 65.4 ± 28.6 g. The fish in both experiments were statistically similar in both length and weight (t test, $P = 0.9147$ and 0.5687, respectively). All fish had undergone morphological changes associated with smoltification: partial or full loss of parr marks, silvering, and darkening of fin margins. Hatchery cohorts are historically released at the time of these experiments, further supporting that these fish were preparing for migration into salt water. Experiments were conducted at Oregon State University's Oak Creek Laboratory, Corvallis, Oreg. As needed, fish were transported for 15 min from the Fish Performance Laboratory in 130-L plastic cans supplied with oxygen. No fish died during or after transport. Water temperature at the Oak Creek Laboratory ranged from 8 to 10 °C.

Saltwater preference tanks

Saltwater preference experiments were carried out in four, 757-L rectangular tanks (1.83 m × 0.66 m × 0.60 m) with Plexiglas® front windows and flowing (3 L·min^{-1}) well water. Each was enclosed by a black plastic curtain with holes cut out to allow for visual observation. Fluorescent lights were suspended above each tank. Light was diffused by fiberglass netting on frames suspended below the bulbs. During experiments, salt water (30 ppt) was introduced into the bottom of each tank from one of two header tanks. Header tanks were 1-m-diameter, circular tanks (450 L) and were elevated approximately 1.5 m above the bottom of the experimental tanks. Each header was connected to one of the preference tanks by plastic pipes running along the bottom of the experimental tanks. These pipes had small holes drilled in two rows that allowed salt water to slowly diffuse to the tank bottom.

Fish transported to the Oak Creek Laboratory were randomly placed into preference tanks and held in aerated, flowing water for 48 h. This allowed fish to acclimate to the new tank conditions. No fish died during acclimation. Preliminary work found that after 48 h fish began feeding normally, so we considered them to be acclimated after this time. When fish were first introduced to the tank, they generally settled on the tank bottom in a tight group. Once ac-

© 2003 NRC Canada

climated, this behavior was not observed. Fish were not observed resting directly on the tank bottoms. Instead, fish tended to position themselves 5–30 cm off the bottom. Fish were dispersed throughout the tanks and actively explored all areas of the tank, including the surface. Tight schooling of the fish was never observed. The photoperiod was set to the ambient light cycle. Fish were not fed during acclimation or experiments to reduce disturbance to the tank.

After acclimation, 379 L of salt water was mixed in each header tank using Instant Ocean® artificial salt and was aerated. Dissolved oxygen levels were similar between experimental tanks and header tanks and were near saturation. Ten minutes before saltwater introduction, water supply and aeration were turned off to prevent mixing. This lack of flow in the tank also removed flow as a possible directive stimulus. The valves from the header tanks were then opened and salt water began to flow into the bottom of the preference tanks, pushing the lighter fresh water out of the top-draining standpipe. This created a stable saltwater layer in the bottom of the water column with a freshwater layer on top. The halocline was visible, so it was easy to distinguish whether fish were in salt or fresh water. The same person (C.S.P.) made all observations to eliminate observer bias as a confounding factor. Every 10 min the number of fish holding in fresh or salt water was observed and recorded. Care was taken to ensure that the positions of all fish were accounted for. This interval was chosen because at this time the saltwater layer had increased to 5 cm in depth, which was about the height of the fish at this size. Thus, at the first observation time, it was possible for a fish to be holding completely in salt water. Some fish did not hold in one layer or the other, but instead moved between the two layers. These were tallied separately from the other two behavioral groups. A fish was considered to be moving between the layers if it left the layer in which it was seen at the beginning of each counting observation one or more times. Behavioral counts took less than 1 min to tally. Although individual fish were not marked, there were few enough fish in the tank that the movement patterns (i.e., holding in a layer or moving between them) of each fish could be readily assessed within this time. Fish that were holding in either the fresh- or salt-water layer were easy to count as they typically did not move about quickly. Thus, fish moving vertically between the layers could easily be distinguished and counted. It took just under 1 h for all of the salt water to flow into the tanks. At this time, the bottom half of the water column (30 cm deep) was saline and the top half was fresh. Observations were continued for another 60 min. Preliminary experiments with dyed salt water showed that the halocline was stable for several days when no fish were present, and no mixing occurred. Early tests also found that with fish in the tanks (and some potential mixing from swimming), salinity in the top half remained below 3 ppt for at least 24 h.

Experiment I: effects of a mild chasing stress on saltwater preference of juvenile chinook salmon

We conducted this experiment to determine the effects of a mild stressor, which simulated a fish being pursued by a predator, on the saltwater preference of chinook salmon. A preliminary experiment was conducted to establish that a physiological stress response could be elicited by chasing fish with a large net. On 27 January 1999, 15 fish were stocked into each of two preference tanks and allowed to acclimate for 48 h. In one tank, fish were chased with a dip net (opening was 30 cm × 45 cm) for 2 min. Fish were not held in the net or removed from the water. Fish in the other tank served as controls and were not disturbed. After 45 min, fish from both tanks were quickly (~1 min) netted out and immediately killed by overdose of tricaine methanesulfonate (200 $mg \cdot L^{-1}$). Blood was collected from all fish in heparinized capillary tubes after severing the caudal peduncle. The blood was centrifuged, plasma was collected, and samples were stored at –80 °C until analysis. Plasma cortisol levels were assessed as an indicator of stress using a radioimmunoassay (Foster and Dunn (1974) and modified by Redding et al. (1984)).

On 21, 25, and 29 March and 2 April 1999, 52 naive fish were transported to the Oak Creek Laboratory, divided equally between the four preference tanks, and allowed to acclimate for 48 h. On each experimental day, four tanks could be observed; however, only two could be viewed simultaneously. Therefore, two consecutive sets of experiments were done per day, each consisting of one control (not chased) and one treatment (chased). In total, eight tanks with chased fish and eight tanks with unchased fish were observed. Tanks were alternately assigned over all the experiments to serve for either control or treatment. After acclimation, fish in treatment tanks were chased with a dip net for 2 min as described above. Salt water was then introduced and fish positions were recorded as previously described.

Experiment II: effects of a handling stress on saltwater preference of juvenile chinook salmon and response to avian model

This experiment was conducted to investigate the effects of a more severe handling stressor on saltwater preference and to determine the response of stressed fish to an avian predator. On 2, 7, and 9 February 2000, 40 naive fish were transported to the Oak Creek Laboratory, equally divided between the four preference tanks, and allowed to acclimate for 48 h. The design of the experiment was similar to that used in experiment I. After acclimation, fish in treatment tanks were quickly removed by dip net and placed for 15 min in a 21-L bucket containing 8 cm of water and an airstone. They were then returned to the preference tank, salt water was introduced, and fish positions were recorded. In the treatment tanks, once all salt water had entered the tank, an avian predator model was suddenly introduced through a hole in the plastic curtain. The model was constructed to mimic a tern (*Sterna* sp.), a surface-feeding bird common in estuaries and known to feed on salmonid smolts (Collis et al. 2001). The model was cut from 2.5-cm-thick Styrofoam, covered with white colored tape and painted to resemble a bird viewed from below. The model was 36 cm long from beak to tail, its wingspan was 31 cm, and it was suspended by clear monofilament line from a thin, 1.3-m-long pole. The model was suspended over the tank for 3 s, dropped momentarily on the mesh tank cover (8 cm above water surface), and then held above the tank for another second before being removed from the tank area. Tank covers were left in place so that conditions in the tank after the stress experience were identical to conditions before stress and to

© 2003 NRC Canada

Table 1. Saltwater (SW) preference of chased and control juvenile chinook salmon in experiment I.

Treatment	Date	Tank	Percent of fish holding in SW after: 60 min	120 min	Minutes until >50% fish hold in SW
Control	23 March	1	100	100	20
		2	100	100	10
	27 March	1	100	86	20
		2	100	100	20
	31 March	1	69	77	60
		2	100	100	20
	4 April	1	100	100	20
		2	100	100	20
Chased	23 March	1	31	54	110
		2	100	100	30
	27 March	1	46	54	80
		2	23	62	120
	31 March	1	77	69	50
		2	54	69	60
	4 April	1	69	77	50
		2	100	69	20
Mean ± SD	Control		96 ± 11 a	95 ± 9 a	24 ± 15 a
	Chased		63 ± 29 b	69 ± 15 b	65 ± 36 b

Note: The time until at least 50% of fish were holding in salt water is also given. Means in the same column with different letters are significantly different ($p < 0.05$). SD, standard deviation.

control tanks. Prior observations found that fish were more oriented toward the tank bottom when covers were not used, and we wanted to avoid this as a potential confounding factor. After the model was presented, fish positions were recorded immediately after the model was removed from the tank area and then every 10 min for another hour. Observations of control fish (no stress and no model) were conducted for 1 h during saltwater introduction and for 1 h after introduction.

Statistical analysis

Each tank was considered an independent replicate. For each tank, the percentages of fish holding in salt and fresh water or moving between the layers at 60 and 120 min were calculated. These data were arcsine transformed to make them continuous. Multifactor analysis of variance (ANOVA, $P < 0.05$) was used to determine any treatment, tank, and date effects. In both experiments, the only significant factor was treatment; therefore, the replicates for each of the two treatments were pooled for one-way ANOVA. If data were skewed, the nonparametric Kruskal–Wallis comparison of medians was performed to determine treatment effect. For pairwise comparisons, post-hoc t tests were used.

Results

Experiment I: effects of a mild chasing stress on saltwater preference of juvenile chinook salmon

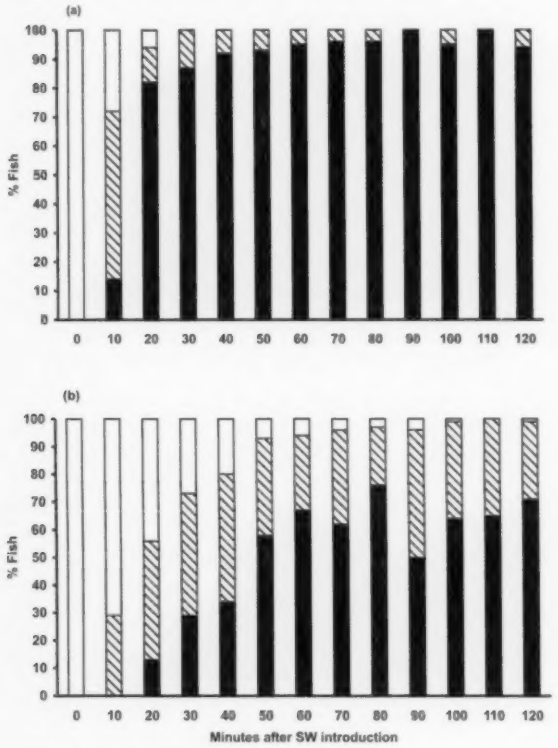
The preliminary stress experiment found that chasing fish with a dip net for 2 min did elicit a stress response. After 45 min, the mean cortisol concentration of the chased fish was 145 ± 30.8 (± standard deviation (SD)) ng·mL^{-1} compared with 60 ± 39.0 ng·mL^{-1} for controls (t test, $P < 0.0001$). The latter concentration is consistent with increased cortisol levels found in smolted chinook salmon.

When salt water was first introduced and perceived, control fish initially avoided it and then gradually began moving into the saltwater layer. They usually spent 10–20 min moving between the two layers. Some fish immediately entered and remained in salt water, which often meant holding in a layer <5 cm from the bottom. Once a fish held in salt water, it usually did not return to fresh water for the duration of the experiment. As the saltwater layer deepened, fish holding there moved throughout the layer. Most fish that avoided salt water and chose to hold in fresh water had explored the saltwater layer multiple times. Fish holding in both salt and fresh water were frequently observed swimming to the halocline, but not across it. A few fish that were "undecided" would position themselves directly on the halocline as the saltwater layer moved up the water column. Stressed fish generally settled near the bottom of the tank after being chased. However, they quickly moved up in the water column in response to the addition of salt water. Chased fish were less likely to enter and hold in the saltwater layer, as described below.

No date or tank effects were found (ANOVA, $P = 0.3454$ and 0.2014, respectively), so the eight replicates of chased or unchased fish were pooled for the four dates. After 60 min, 63 ± 29% of fish that had been chased were holding in salt water compared with 96 ± 11% of control fish (Table 1; Fig. 1; Kruskal–Wallis, $P = 0.0128$). This trend continued, and after 2 h, 69 ± 15% of chased fish and 95 ± 9% of controls were holding in the saltwater layer (Kruskal–Wallis, $P = 0.0035$). In control tanks, half of the fish had entered and remained in salt water within 24 ± 15 min compared with 65 ± 36 min for chased fish (Kruskal–Wallis, $P =$

© 2003 NRC Canada

Fig. 1. (*a*) Mean percentage of control fish holding in fresh water (FW) and salt water (SW) or moving between the layers in experiment I. Time = 0 represents the beginning of saltwater introduction. (*b*) Mean percentage of chased fish holding in fresh and salt water or moving between the layers in experiment I. Time = 0 represents the beginning of saltwater introduction. Fish in fresh water, open bars; fish moving between the layers, hatched bars; fish in salt water, solid bars.



0.0056). Not only did fewer chased fish choose to remain in salt water, but it also took them longer to make that choice.

Experiment II: effects of a handling stress on saltwater preference and response to avian model of juvenile chinook salmon

General behavior patterns of stressed and control were similar to fish in experiment I. No date or tank effects were found (ANOVA, $P = 0.7917$ and 0.9883, respectively), and replicates from the two treatments were pooled for the three dates. In all six control tanks, 100% of the fish were holding in salt water after 60 min (Table 2; Fig. 2*a*), and more than half of them held there within 25 ± 8 min. After all of the salt water was introduced, only 20 ± 13% of stressed chinook were holding in salt water (Table 2; Fig. 2*b*; Kruskal–Wallis, $P = 0.0019$). In none of the tanks did more than half of the stressed fish hold in salt water after 1 h. Once the avian model was dropped, all of the stressed fish holding in fresh water or moving between the layers immediately moved into the saltwater layer (Fig. 2*b*). In five of the six tanks, some of the fish began returning to the freshwater layer within 10 min of exposure to the predator model. After 1 h, only 26 ± 11% of stressed fish remained in the salt water. In one tank (9 February, tank 1), 90% of the stressed fish remained in the saltwater layer for 1 h after exposure to the model. By comparison, 100% of control fish were holding in salt water 1 h after saltwater introduction (Kruskal–Wallis, $P = 0.0020$).

Discussion

Our experiments found that both a mild chasing stressor and a more severe confinement stressor decreased the willingness of juvenile spring chinook salmon to remain in salt water at a developmental stage when unstressed fish prefer salt to fresh water. Although our experiments were conducted in different years and with two stocks of fish, we believe that genetic similarity between the stocks and the behavioral similarity of saltwater preference exhibited by control fish in the two experiments indicate that general comparisons can be made between the two experiments. The mild chasing stressor evoked less of a response in terms of saltwater preference. In experiment I, about half of the chased fish did not hold in salt water. Although a small percentage of these fish completely avoided salt water and held in the freshwater layer (about 5%), most of them retained some orientation toward high salinity. Throughout the observation period, 30–40% of the chased fish moved continuously between the two layers. It is important to note that although they did not hold in salt water, they did not necessarily avoid it. In contrast, 20–40% of stressed chinook salmon in experiment II held in the freshwater layer and did not move into the saltwater layer even briefly. The percentage of stressed fish holding in salt water was highest immediately after the avian predator model was presented, but within 20 min, half of the fish had either returned to the fresh water or resumed moving between the layers. Although the stressed fish retained the ability to perceive a threat and displayed appropriate avoidance behavior by moving into deeper water, their avoidance response was transient. In only one tank did most of the stressed fish remain in the saltwater layer for an extended period after the model was introduced. These fish remained tightly grouped for the hour after the model was presented. Schooling behavior in prey fish often increases in the presence of predatory threat and is a group response to perceived danger (Pitcher 1986; Diana 1995). This behavior contrasted sharply with that of the other stressed fish for which behavior was more influenced by each individual's physiological state.

Stress is known to cause electrolyte imbalance in salmonids (Eddy 1981; McDonald and Milligan 1997) and we suggest that this is the most likely explanation for the avoidance of salt water by stressed fish in our experiments. Stressed fish have higher water and ion flux across the gill epithelium (McDonald and Milligan 1997). Freshwater fish tend to lose electrolytes and gain water, whereas the opposite occurs in saltwater-adapted species (Mazeaud et al. 1977). Redding and Schreck (1983) subjected yearling coho salmon acclimated in fresh water to a confinement stress and immediately placed them in seawater. Plasma sodium concentration

© 2003 NRC Canada

Table 2. Saltwater (SW) preference of stressed and control juvenile chinook salmon in experiment II.

Treatment	Date	Tank	Percent of fish holding in SW after: 60 min	120 min
Control	4 February	1	100	100
		2	100	100
	9 February	1	100	100
		2	100	100
	11 February	1	100	100
		2	100	100
Stress + avian model	4 February	1	10	10
		2	30	20
	9 February	1	40	90
		2	10	40
	11 February	1	10	30
		2	20	30
Mean ± SD		Control	100 ± 0 a	100 ± 0 a
		Stress	20 ± 13 b	37 ± 28 b

Note: An avian predator model was presented to stressed fish 60 min after the beginning of saltwater introduction and all stressed fish were in the SW layer. Means in the same column with different letters are significantly different ($p < 0.05$). SD, standard deviation.

and osmolarity remained elevated for 24 h, and there was a high mortality rate for these fish.

Although isotonic concentrations of salt have been found to be beneficial to fish recovering from stress (Wedemeyer 1972; Strange and Schreck 1980; Redding and Schreck 1983), high salinity may be a serious threat to recovery and survival. For example, Järvi (1989*b*) found that Atlantic salmon exposed concomitantly to osmotic stress and exposure to a predator were nearly twice as likely to be eaten compared with fish that were exposed to each stressor alone. The saltwater challenge test conducted at Lower Granite Dam found that spring chinook salmon mortality in saltwater challenge tests was positively related to the amount of stress that the fish had experienced while passing through collection and raceway facilities (Matthews et al. 1986). Both of these studies suggest that when stressed fish first encounter salt water, it may be perceived as an additional stressor.

Avoidance of salt water by stressed chinook salmon has been reported in salmonids (Kruzynski and Birtwell 1994). Chinook salmon exposed to the toxicant TCMTB were placed together with predators in a vertically stratified (fresh over salt water) 15 500-L tank. Preliminary experiments found that although fish survived toxicant exposure in fresh water, subsequent exposure to seawater resulted in 90% mortality. Although nonexposed chinook salmon held in the saltwater layer, exposed fish were typically observed holding in fresh water or just below the halocline. Exposed fish also showed reduced orientation to cover and swam erratically. As a result of these behavioral changes, predation by yellowtail rockfish was greater on exposed fish.

Chinook salmon suffering from BKD also showed a decreased preference for salt water under experimental conditions similar to those of this study (Price and Schreck 2003). Only 31% of sick fish held in salt water, and preference was correlated with severity of infection. Fish with BKD typically exhibit high mortality in salt water because of decreased osmocompetence (Moles 1997), despite the fact that the disease does not seem to inhibit the smolting process (Mesa et al. 1999).

Another study in our laboratory (C.B. Schreck, unpublished data) investigated the delayed behavioral effects of multiple stressors on smolted chinook salmon. In this study, fish were subjected over 16 days to a series of eight severe handling stressors to simulate passage through multiple hydroelectrical dams, and a physiological stress response was observed, as indicated by elevated cortisol concentrations. Three hours after the last stressor, cortisol levels had returned to baseline values. After a 2-week recovery, saltwater preference tests were performed on multiple-stressed fish and unstressed controls. Over 90% of the control fish held in salt water compared with only 30% of stressed fish. These percentages are consistent with the results from the present study. Although recovery of the primary physiological responses from the stress occurred within hours, delayed behavioral effects were still apparent more than 2 weeks later.

In the present experiments, control fish quickly made the choice to hold in salt water, whereas stressed fish likely perceived the salt water as an additional stressor. Thus, stressed fish were forced to make a choice between two conflicting physiological motivations. Chinook salmon in these experiments were in the latter stages of smoltification, which is defined as the sum of physiological, morphological, and behavioral changes that anadramous salmonids undergo to prepare for ocean residence (Folmar and Dickhoff 1980; Wedemeyer et al. 1980; Hoar 1988). Although their ultimate physiological state would tend to facilitate entry into salt water, the proximate physiological restrictions imposed by stress seemed more important in determining their preference behavior. Furthermore, the degree of behavioral shift reflected the severity of the stressor.

The stressed chinook salmon were again faced with conflicting stimuli when an additional stressor (i.e., the avian

© 2003 NRC Canada

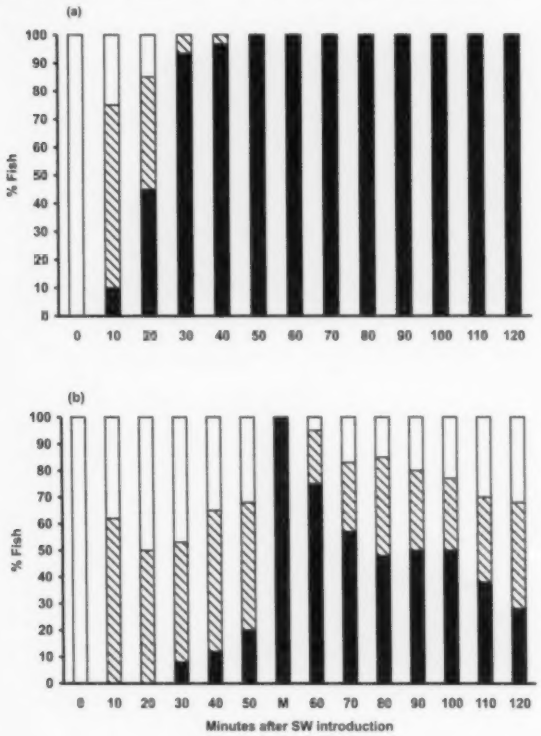


Fig. 2. (*a*) Mean percentage of control fish holding in fresh water (FW) and salt water (SW) or moving between the layers in experiment II. Time = 0 represents the beginning of saltwater introduction. (*b*) Mean percentage of stressed fish holding in fresh and salt water or moving between the layers in experiment II. At 59 min (represented by "M" on the graph), an avian predator model was dropped. Time = 0 represents the beginning of saltwater introduction. Fish in fresh water, open bars; fish moving between the layers, hatched bars; fish in salt water, solid bars.

model) was introduced. By moving into the saltwater layer, fish seemingly made the appropriate choice with regards to immediate threat. However, they chose not to remain in salt water once the model had been removed. In preliminary trials using a mild chasing stressor, fish that had initially avoided salt water also responded to overhead disturbance by moving into the lower, saltwater layer. These fish typically remained in salt water for up to 1 h, but this was not investigated further in formal experiments. However, this difference in response behavior reinforces our observation that the severity of the initial stressor affects the willingness of fish to hold in salt water.

Our results suggest that if juvenile chinook salmon are stressed during the estuarine phase of outmigration, their orientation toward salt water may be compromised. Although it is known that salmonids can orient to salinity gradients (McInerney 1964), little is known about how this environmental factor may be regulating vertical distribution of outmigrating fish in estuaries. Based on our laboratory findings, one might expect that mildly stressed fish would only briefly delay volitional entry into seawater. More severely stressed fish might avoid salt water altogether. In either case, this behavior is likely maladaptive and would expose fish to increased predation risk. Many estuaries have a stratified water column with less-dense fresh water floating on the denser salt water, and outmigrating salmon have been reported to display surface orientation during outmigration and under laboratory conditions (Birtwell and Kruzynski 1989).

Avoidance of salt water in a stratified estuary has been reported for outmigrating juvenile chum salmon in Japan (Iwata and Komatsu 1984). Laboratory experiments attributed this behavior to saltwater acclimation and improved osmoregulatory performance. If the freshwater lens is very shallow, salmonid smolts using it as a refuge from osmoregulatory stress may be more susceptible to avian predators feeding at or near the surface. Stressed fish would be compromised both by their position in the upper freshwater lens and by a stress-induced decrease in predator-avoidance response.

This study did not investigate the time that it took for stressed fish to behaviorally "recover" and enter salt water. Although short-term avoidance of salt water may be adaptive in terms of decreasing osmoregulatory stress, extended avoidance might be deleterious. Spring chinook salmon in the Columbia River estuary are moving through the estuary within one or two tidal cycles, so they must quickly acclimate to full-strength salt water and ocean conditions. Salmon with extended estuarine residence times could also be impacted if their use of the freshwater layer as an osmoregulatory refuge is extended. An efficient shift from fresh to salt water may be a critical factor in determining early ocean survival for salmon. Speculatively, fish that experience physiological or osmoregulatory stress in the estuarine environment may be more likely to succumb to adverse conditions after ocean entry.

Although management practices can by no means eliminate all potential stressors for outmigrating juvenile chinook salmon, efforts to improve overall fish quality or condition may maximize the ability of these fish to appropriately respond to environmental stimuli (Wedemeyer et al. 1980; Iwama 1992). For example, our results suggest that ensuring that the fish released from hatcheries have reached a sufficient stage of smoltification will improve their physiological motivation to enter seawater. Improved engineering of dam passage facilities to reduce stress to fish during the riverine phase of outmigration would be advantageous for decreasing delayed stress effects. Natural stressors such as predators, toxins, or environmental perturbations would also be expected to elicit a behavioral stress response. Increased awareness of the interactions between physiology, stress, and behavior and experimental designs incorporating the effects of stress at multiple scales will improve our knowledge of the ecological relevance of stress.

Acknowledgments

We thank the U.S. Army Corps of Engineers for the funding to pursue this research, Rob Chitwood for assistance with fish husbandry, Dr. Cliff Pereira for statistical advice, and Beth Siddens for conducting the cortisol assays. The comments of two reviewers were useful in improving the

© 2003 NRC Canada

manuscript. This is Technical Report No. 11667 of the Oregon Agricultural Experiment Station.

References

Adams, S.M. (*Editor*). 1990. Biological indicators of stress in fish. Am. Fish. Soc. Symp. No. 8.

Birtwell, I.K., and Kruzynski, G.M. 1989. *In situ* and laboratory studies on the behavior and survival of Pacific salmon (genus *Oncorhynchus*). Hydrobiologia, **188/189**: 543–560.

Collis, K., Roby, D.D., Craig, D.P., Ryan, B.A., and Ledgerwood, R.D. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. Trans. Am. Fish. Soc. **130**: 385–396.

Diana, J.S. 1995. Biology and ecology of fishes. Cooper Publishing Group LLC, Carmel, Ind.

Eddy, F.B. 1981. Effects of stress on osmotic and ionic regulation in fish. *In* Stress and fish. *Edited by* A.D. Pickering. Academic Press Inc., New York. pp. 77–102.

Folmar, L.C., and Dickhoff, W.W. 1980. The parr–smolt transformation (smoltification) and seawater adaptation in salmonids: a review of selected literature. Aquaculture, **21**: 1–37.

Folmar, L.C., Craddock, D.R., Blackwell, J.W., Joyce, G., and Hodgins, H.O. 1981. Effects of petroleum exposure on predatory behavior of coho salmon (*Oncorhynchus kisutch*). Bull. Environ. Contam. Toxicol. **27**: 458–462.

Foster, L.C., and Dunn, R.T. 1974. Single-antibody technique for radioimmunoassay of cortisol in extracted serum or plasma. Clin. Chem. **20**: 365–368.

Hoar, W.S. 1988. The physiology of smolting salmonids. *In* Fish physiology. Vol. XIB. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego, Calif. pp. 275–343.

Iwama, G.K. 1992. Smolt quality: a special section. World Aquacult. **23**: 38–39.

Iwama, G.K., Pickering, A.D., Sumpter, J.P., and Schreck, C.B. (*Editors*). 1997. Fish stress and health in aquaculture. Society for Experimental Biology Seminar Series No. 62, Cambridge University Press, Cambridge.

Iwata, M., and Komatsu, S. 1984. Importance of estuarine residence for adaptation of chum salmon (*Oncorhynchus keta*) fry in seawater. Can. J. Fish. Aquat. Sci. **41**: 744–749.

Järvi, T. 1989*a*. The effects of osmotic stress on the anti-predator behavior of Atlantic salmon smolts: a test of the 'maladaptive anti-predator behavior' hypothesis. Nord. J. Freshw. Res. **65**: 71–79.

Järvi, T. 1989*b*. Synergistic effect on mortality in Atlantic salmon, *Salmo salar*, smolt caused by osmotic stress and presence of predators. Environ. Biol. Fishes, **26**: 149–152.

Jones, K.A., and Hara, T.J. 1988. Behavioral alterations in Arctic charr (*Salvelinus alpinus*) briefly exposed to sublethal chlorine levels. Can. J. Fish. Aquat. Sci. **45**: 749–753.

Jones, K.A., Brown, S.B., and Hara, T.J. 1987. Behavioral and biochemical studies of onset and recovery from acid stress in Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. **44**: 373–381.

Kruzynski, G.M., and Birtwell, I.K. 1994. A predation assay to quantify the ecological significance of sublethal responses of juvenile chinook salmon (*Oncorhynchus tshawytscha*) to the antisapstain fungicide TCMTB. Can. J. Fish. Aquat. Sci. **51**: 1780–1790.

Matthews, G.M., Park, D.L., Achord, S., and Ruehle, T.E. 1986. Static seawater challenge test to measure relative stress levels in spring chinook salmon smolts. Trans. Am. Fish. Soc. **115**: 236–344.

Mazeaud, M.M., Mazeaud, F., and Donaldson, E.M. 1977. Primary and secondary effects of stress in fish: some new data with a general review. Trans. Am. Fish. Soc. **106**: 201–212.

McCormick, S.D., Shrimpton, J.M., Carey, J.B., O'Dea, M.F., Sloan, K.E., Moriyama, S., and Björnsson, B.Th. 1998. Repeated acute stress reduces growth rate of Atlantic salmon parr and alters plasma levels of growth hormone, insulin-like growth factor I and cortisol. Aquaculture, **168**: 221–235.

McDonald, G., and Milligan, L. 1997. Ionic, osmotic and acid–base regulation in stress. *In* Biological indicators of stress in fish. *Edited by* S.M. Adams. Am. Fish. Soc. Symp. No. 8. pp. 119–144.

McEwen, B.S. 1998. Protective and damaging effects of stress mediators. N. Engl. J. Med. **338**: 171–179.

McInerney, J.E. 1964. Salinity preference: an orientation mechanism in salmon migration. J. Fish. Res. Board Can. **21**: 995–1018.

Mesa, M.G. 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile chinook salmon. Trans. Am. Fish. Soc. **123**: 786–793.

Mesa, M.G., Maule, A.G., Poe, T.P., and Schreck, C.B. 1999. Influence of bacterial kidney disease on smoltification in salmonids: is it a case of double jeopardy? Aquaculture, **174**: 25–41.

Moles, A. 1997. Effect of bacterial kidney disease on saltwater adaptation of coho salmon smolts. J. Aquat. Anim. Health, **9**: 230–233.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grand, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., and Waples, R.S. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-35.

Olla, B.L., Davis, M.W., and Schreck, C.B. 1992. Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile coho salmon. Trans. Am. Fish. Soc. **121**: 544–547.

Pickering, A.D. (*Editor*). 1981. Stress and fish. Academic Press Inc., New York.

Pickering, A.D., Pottinger, T.G., and Christie, P. 1982. Recovery of the brown trout, *Salmo trutta* L., from acute handling stress: a time-course study. J. Fish Biol. **20**: 229–244.

Pitcher, T.J. 1986. Functions of shoaling behavior in teleosts. *In* The behavior of teleost fish. *Edited by* T.J. Pitcher. The Johns Hopkins University Press, Baltimore, Md. pp. 294–337.

Price, C.S., and Schreck, C.B. 2003. Effects of bacterial kidney disease on saltwater preference of juvenile spring chinook salmon, *Oncorhynchus tshawytscha*. Aquaculture, **222**: 331–341.

Redding, J.M., and Schreck, C.B. 1983. Influence of ambient salinity on osmoregulation and cortisol concentration in yearling coho salmon during stress. Trans. Am. Fish. Soc. **112**: 800–807.

Redding, J.M., Schreck, C.B., Birks, E.B., and Ewing, R.D. 1984. Cortisol and its effects on plasma thyroid hormone and electrolyte concentrations in fresh water and during seawater acclimation in yearling coho salmon. *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. **56**: 146–155.

Schreck, C.B. 1990. Physiological, behavioral, and performance indicators of stress. *In* Biological indicators of stress in fish. *Edited by* S.M. Adams. Am. Fish. Soc. Symp. No. 8. pp. 29–37.

Schreck, C.B. 2000. Accumulation and long-term effects of stress in fish. *In* The biology of animal stress. *Edited by* G.P. Moberg and J.A. Mench. CAB International, Wallingford. pp. 147–158.

Schreck, C.B., Olla, B.L., and Davis, M.W. 1997. Behavioral responses to stress. *In* Fish stress and health in aquaculture. *Edited by* G.K. Iwama, A.D. Pickering, J.P. Sumpter, and C.B. Schreck. Society for Experimental Biology Seminar Series No. 62, Cambridge University Press, Cambridge. pp. 145–170.

© 2003 NRC Canada

Selye, H. 1950. Stress and the general adaptation syndrome. Br. Med. J. **1**: 1383–1392.

Sigismondi, L.A., and Weber, L.J. 1988. Changes in avoidance response time of juvenile chinook salmon exposed to multiple acute handling stresses. Trans. Am. Fish. Soc. **117**: 196–201.

Strange, R.J., and Schreck, C.B. 1980. Seawater and confinement alters survival and cortisol concentration in juvenile chinook salmon. Copeia, **1980**: 351–353.

Wedemeyer, G.A. 1972. Some physiological consequences of handling stress in the juvenile coho salmon (*Oncorhynchus kisutsch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **33**: 2699–2702.

Wedemeyer, G.A., Saunders, R.L., and Clarke, W.C. 1980. Environmental factors affecting smoltification and early marine survival of anadramous salmonids. Mar. Fish. Rev. **42**: 1–14.

Wedemeyer, G.A., Barton, B.A., and McLeay, D.J. 1990. Stress and acclimation. *In* Methods for fish biology. *Edited by* C.B. Schreck and P.B. Moyle. American Fisheries Society, Bethesda, Md. pp. 451–489.

© 2003 NRC Canada

Intraspecific density dependence in the dynamics of zooplankton under hypertrophic conditions

Steven Declerck, Vanessa Geenens, Nicole Podoor, José Maria Conde Porcuna, and Luc De Meester

Abstract: Intraspecific interactions may limit population growth of small cladoceran taxa under food-rich, hypertrophic conditions. Multiple-regression models significantly explained a large proportion of the variation in the body size adjusted fecundity and population growth rate of crustacean zooplankton taxa in a shallow, hypertrophic lake. The results of partial correlation analyses suggested exploitative competition to have only limited significance in determining the zooplankton dynamics. The analyses also revealed strong negative relationships between biomass and both body size adjusted fecundity and population growth rate within most taxa. Most of these relationships cannot be explained by food shortage or predation and suggest alternative mechanisms such as chemically mediated, intraspecific interference competition or life history shifts.

Résumé : Les interactions intraspécifiques peuvent limiter la croissance de la population chez des taxons de cladocères de petite taille dans des conditions hypertrophiques de nourriture abondante. Des modèles de régression multiple expliquent de façon significative une importante proportion de la variation de la fécondité ajustée en fonction de la taille et du taux de croissance de la population chez des taxons de crustacés zooplanctoniques dans un lac hypertrophe peu profond. Les résultats d'analyses de corrélation partielle laissent croire que la compétition d'exploitation ne joue qu'un rôle limité dans la dynamique du zooplancton. Ces analyses démontrent aussi l'existence de fortes relations négatives entre la biomasse, d'une part, et la fécondité ajustée en fonction de la taille et le taux de croissance de la population, d'autre part, chez la plupart des taxons. La plupart de ces relations ne s'expliquent pas par une carence de nourriture ou par la prédation et il y a lieu de croire à l'existence de mécanismes de rechange, tels que la compétition d'interférence au moyen de substances chimiques ou les déphasages des cycles biologiques.

[Traduit par la Rédaction]

Introduction

Along a gradient of increasing nutrient levels, both total fish biomass and the proportion of planktivores in fish communities tend to increase (Persson et al. 1988; Jeppesen et al. 2000). Concurrently, submersed vegetation, an important refuge for zooplankton against fish predation (Moss et al. 1998), tends to decrease (Hough et al. 1989). As fish planktivory is highly size selective, this may explain why small taxa tend to dominate the zooplankton communities of eutrophic and hypertrophic water bodies (Hessen et al. 1995; Jeppesen et al. 2000). Given its predominance, the importance of small zooplankton in key processes of eutrophic systems (such as grazing, nutrient cycling, or energy transfer) can therefore be expected to be more important than that of large zooplankton. An important question is what factors limit the population growth of such small zooplankton in nutrient-rich lakes. Fish predation plays a major role in eliminating large zooplankton taxa, but its importance in the top-down regulation of small taxa is much less obvious. On the contrary, fish predation may stimulate population growth of small zooplankton taxa by reducing invertebrate predation or by decreasing the intensity of competitive interactions with large zooplankton (Sluzarczyk 1997; Moss et al. 1998). Food availability should be high, although only very few studies have evaluated food limitation as a population growth limiting mechanism in eutrophic systems (Boersma and Vijverberg 1994; Boersma 1995). Most studies on exploitative competition between cladocerans were carried out under laboratory conditions and focused on interactions between large and small taxa (Gliwicz 1990; Achenbach and Lampert 1997). In field studies, competitive interactions be-

Received 12 July 2002. Accepted 29 May 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 5 September 2003.
J17041

S. Declerck.[1,2] Laboratory of Animal Ecology, Zoogeography and Nature Conservation, University of Gent, K.L. Ledeganckstraat 35, 9000 Gent, Belgium.
V. Geenens. Laboratory of Protistology and Aquatic Ecology, University of Gent, K.L. Ledeganckstraat 35, 9000 Gent, Belgium.
N. Podoor. Laboratory of Ecology, Institute of Botany, KULeuven, Kard. Mercierlaan 92, 3001 Heverlee, Belgium.
J.M. Conde Porcuna. Departamento de Biologia Animal y Ecologia, Universidad de Granada, Campus Fuentenueva s/n, E-18071 Granada, Spain.
L. De Meester. Laboratory of Aquatic Ecology, KULeuven, Ch. de Bériotstraat 32, 3000 Leuven, Belgium.

[1]Corresponding author (e-mail: Steven.Declerck@bio.kuleuven.ac.be).
[2]Present address: Laboratory of Aquatic Ecology, KULeuven, Ch. de Bériotstraat 32, 3000 Leuven, Belgium.

 doi: 10.1139/F03-077 © 2003 NRC Canada

tween zooplankton taxa have mostly been inferred from negative correlations between the density and fecundity of populations, without taking into account the dynamics of food availability (Matveev 1983; Bengtsson 1993; Boersma 1995). Such correlations may be misleading, as a growing body of experimental evidence suggests that cladoceran populations may show inter- or intra-specific interference, irrespective of the availability of food (Matveev 1991; Kirk 1998; Burns 2000).

In this study, we analyze the dynamics of the population growth rate and fecundity of small crustacean zooplankton in a hypertrophic lake (Lake Blankaart) during a 4-year period. The general size structure of the zooplankton community and results of former in situ life history and fish exclosure studies (Declerck 2001) indicate a high impact of planktivorous fish predation in the lake. Given that the efficiency of fish predation decreases with decreasing body size of the prey, we aimed to test the hypotheses (1) that the dynamics of populations of small-bodied zooplankton taxa can be adequately explained by models that do not take into account top-down control by fish and (2) that the amount of variation explained by these models increases with decreasing adult body size. Furthermore (3), we wanted to assess the relative importance of the factors limiting population growth of small-bodied crustacean zooplankton taxa, disentangling the effects of exploitative competition, interference competition, and predation by omnivorous copepods.

Material and methods

Sampling

The zooplankton and phytoplankton communities of Lake Blankaart were sampled during a 4-year period (1994–1997). During the growing season (May–September), samples were taken at a fixed station in the pelagic zone of the lake, with time intervals of approximately 2 weeks. Zooplankton was sampled using a Schindler–Patalas plankton trap (12 L). Two zooplankton samples were taken at each of two depths: in the middle of the water column (0.4 m) and just above the lake sediments (1 m). These samples were pooled and fixed with a 5% sucrose formalin solution. Phytoplankton was sampled with a plastic recipient (1 L) at a depth of approximately 0.3 m and fixed with formalin.

Phytoplankton cells were counted with an inverted microscope at magnifications of 30 –400×. For each sample, a total of at least 200 cells were counted and identified up to genus or species level. For the most common taxa, a minimum of 50 cells were measured. The average cell volumes of phytoplankton taxa were estimated by applying formulae of simple geometric shapes. Average cell mass was calculated assuming a specific density of 1 $g \cdot mL^{-1}$. As the edibility of algae for zooplankton may strongly depend on cell size, the biomass was separately calculated for three different phytoplankton size classes: (1) cells with a greatest axial linear dimension (GALD) smaller than 20 µm (PHYTSMALL); (2) cells with a GALD between 20 and 40 µm (PHYTMED); and (3) cells with a GALD larger than 40 µm (PHYTLARGE).

For each abundant zooplankton species, body length of at least 50 haphazardly selected individuals was measured per sampling date. The biomass of zooplankton populations was derived from density estimates, the data on size distribution, and published length versus dry weight regression relationships (Bottrell et al. 1976). In addition, for each sample, fecund *Daphnia* and *Bosmina* individuals were counted and the body length and fecundity (egg number) of at least 30 individuals were assessed. *Daphnia galeata*, *D. cucullata*, and the hybrid *D. galeata* × *cucullata* were discerned by the morphological criteria of Flössner and Kraus (1986). Previous experience with animals of the same lake has shown that the morphological criteria described by Flössner and Kraus (1986) allow a correct assignment of the taxa when cross-checked with molecular markers (S. Declerck, unpublished data).

Statistical analysis

For each time interval, the instantaneous population growth rate r was calculated for each crustacean zooplankton taxon as

$$r = \frac{\ln N_t - \ln N_0}{t}$$

where N_0 and N_t are the population densities (number of individuals·L^{-1}) at the start and end of the time interval, respectively, where t is the duration of the time interval.

Multiple-regression and partial correlation analyses were applied to investigate the relationships between population dynamic parameters of crustacean zooplankton taxa (e.g., population growth rate and fecundity) and their biomass, measures of food availability, and the biomass of potentially competing zooplankton taxa and of predatory copepods. To reduce the number of insignificant variables and to optimise the regression models, the independent variables were subjected to a forward-selection procedure (STATISTICA v5 (StatSoft Inc., Tulsa, Okla.); F to Enter: 1.00; F to remove: 0). To prevent among year trends from interfering with the analyses, all variables were detrended by adding to each value the difference between the mean of the entire 4-year period and the mean of the respective year. Furthermore, analysis of variance (ANOVA) was applied to test for recurrent seasonal patterns. For each variable, the detrended data were grouped according to four periods in the growing season: spring (May), early summer (June), middle summer (July), and late summer (August and September). We assumed that major seasonal trends in the data set should be reflected by differences between these periods. Indeed, seasonal patterns were found for several variables, because spring tended to deviate from the other months. To avoid common seasonal trends that may lead to spurious correlations, analyses were done both including and excluding the May data. In the presentation of our results, we exclude the May data, although inclusion of these data did not affect the major results of the analyses. Regressions were individually checked for outliers.

For the analysis of r, the variables that were subjected to the selection procedure were temperature change during the time intervals (ΔT) and the logarithmically transformed biomass of predominant zooplankton taxa (*D. galeata* (DGAL), *D. galeata* × *cucullata* (HYBR), *D. parvula* (DPAR), *B. longirostris* (BLON), and cyclopoid copepods (CYCL)) and of phytoplankton size classes (PHYTSMALL, PHYTMED,

© 2003 NRC Canada

and PHYTLARGE) at the start of the respective time intervals.

Fecundity is considered a useful indicator of the general condition of field populations of cladocerans (Lampert 1978). However, as the fecundity of a cladoceran is constrained by body size, its assessment may be confounded by variations in body size. To account for this, the average fecundity and the average body size of egg-bearing adults were calculated for each cladoceran taxon at each sampling date. For each taxon, average fecundities were then linearly regressed on average body sizes and the resulting residuals were used as a relative measure of animal condition. In the following text these residuals will be referred to as "adjusted fecundity". Linear regression was used because there was no evidence of strong nonlinearities from an inspection of scatterplots of fecundity on body size. Because of the time needed to produce eggs and the energy storage capacity of cladocerans, fecundity responds to changes in food availability with a time lag. Estimates of such time lags range between 4 and 12 days (Seitz 1980; Matveev 1985; Boersma 1995). For the regression analyses of adjusted fecundities, we estimated the biomass of zooplankton taxa (DGAL, HYBR, DPAR, BLON, CYCL) and of phytoplankton size classes (PHYTSMALL, PHYTMED, and PHYTLARGE) at 8 days before each sampling date by exponential interpolation.

To explore for potential top-down control of phytoplankton by each of the investigated zooplankton taxa, partial correlation coefficients were calculated between the total noncyanobacterial phytoplankton biomass (NONCYAN) and the biomass of DGAL, HYBR, DPAR, BLON, and CYCL. To investigate differential vulnerability of size classes of phytoplankton to zooplankton grazing, partial correlations with the biomass of zooplankton taxa were also calculated for PHYTSMALL, PHYTMED, and PHYTLARGE separately. All of these analyses were performed on logarithmically transformed data.

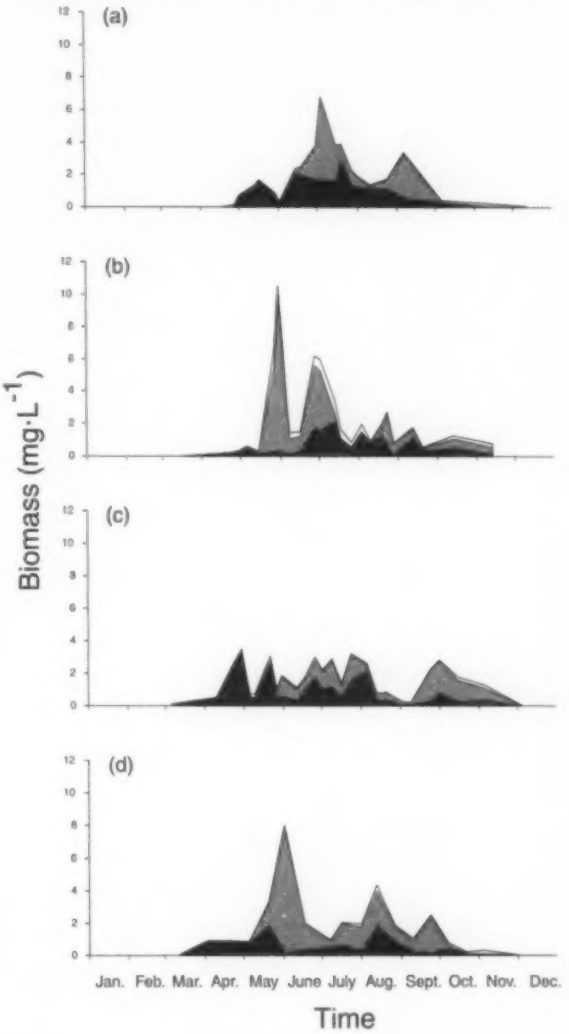
As several multiple-regression analyses were performed per type of dependent variable (e.g., adjusted fecundity and population growth rate of different zooplankton populations; biomass of different phytoplankton fractions), sequential Bonferroni (Rice 1989) was applied on the P levels of the regression models to check for the effect of multiple testing.

Results

Zooplankton community

Annual averages of the total crustacean zooplankton biomass during the growing season (May–September) ranged between ~1.6 and 2.6 mg·L^{-1} (Fig. 1). *Bosmina longirostris* and cyclopoid copepods (*Acanthocyclops robustus*, *Cyclops vicinus*) predominated the zooplankton community of Lake Blankaart during the spring and summer period. The average abundance of *Bosmina* and cyclopoids in the total crustacean zooplankton biomass during the growing season amounted to 41% and 51%, respectively. Although daphnids often dominated during the winter, their relative biomass was much lower during the spring and summer period (average proportion of *Daphnia*: 8%). Total *Daphnia* densities in Lake Blankaart, averaged over the growing season, ranged between 18 and 157 individuals·L^{-1}, depending on the year.

Fig. 1. Biomass (dry weight) of the dominant crustacean zooplankton taxa in Lake Blankaart in (*a*) 1994, (*b*) 1995, (*c*) 1996, and (*d*) 1997. Solid areas represent cyclopoid copepods, shaded areas represent *Bosmina*, and open areas represent *Daphnia*.



The *Daphnia* community mainly consisted of three differently sized taxa (Fig. 2): the relatively large *D. galeata*, the medium-sized hybrid *D. galeata* × *cucullata*, and the relatively small *D. parvula* (average adult body sizes of 1.19, 1.04, and 0.92 mm, respectively). Large *Daphnia* species, such as *D. magna* and *D. pulex*, were occasionally found, but their populations were undetectable during most of the study period.

Population growth rate

Multiple-regression models for all taxa significantly explained population growth rates r (Table 1). The amount of variation explained by the models ranged between 23% and 70% and tended to be considerably lower in the large bodied *D. galeata* than in the other smaller cladoceran taxa (Fig. 3).

© 2003 NRC Canada

Fig. 2. Density of egg-bearing adults of *Daphnia galeata* (solid circles), *D. galeata* × *cucullata* (solid triangles), *D. cucullata* (solid diamonds), and *D. parvula* (open diamonds) in Lake Blankaart in (*a*) 1994, (*b*) 1995, (*c*) 1996, and (*d*) 1997.

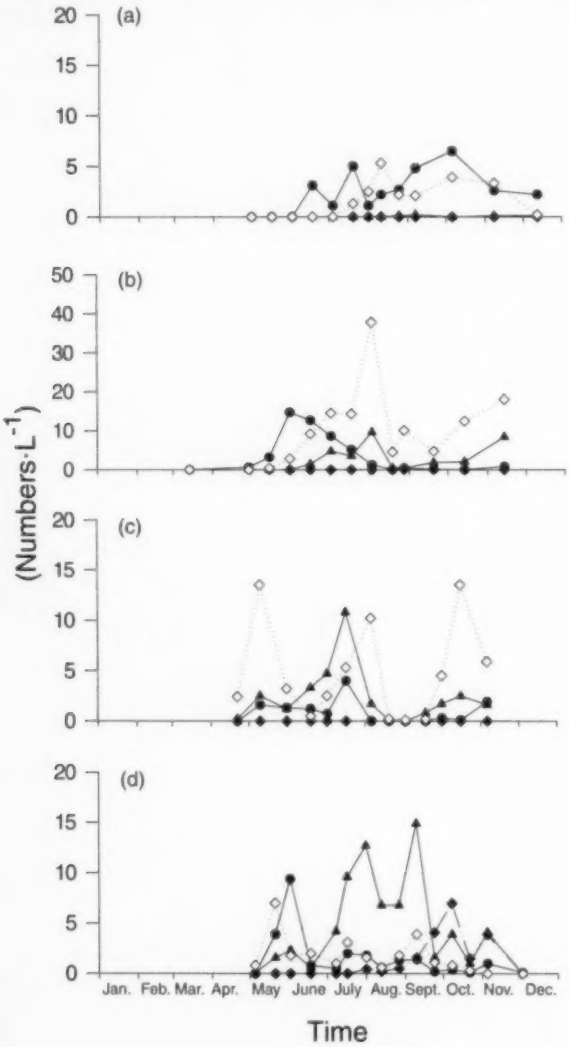
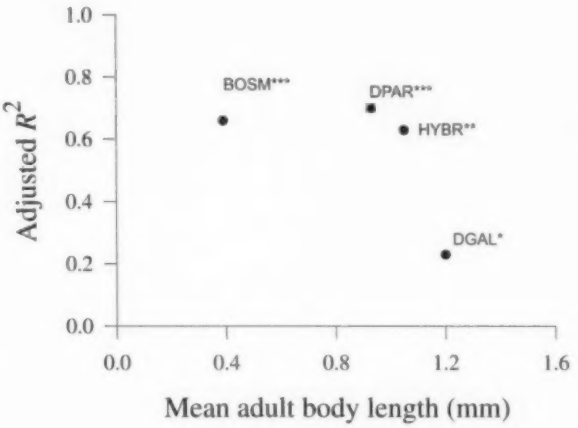


Fig. 3. Relation between the amount of variation in the exponential population growth rate *r* that is explained by the multiple-regression models for the investigated zooplankton taxa (adjusted R^2) and the adult body size of these taxa averaged over the study period. BOSM, *Bosmina longirostris*; DGAL, *Daphnia galeata*; HYBR, *D. galeata* × *cucullata*; DPAR, *D. parvula*. Asterisks near symbols indicate the significance levels of the respective regression models: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.



For all crustacean zooplankton taxa, significantly negative partial correlations were found between the *r* values calculated for time intervals and their population biomass at the start of these time intervals (Table 1; Fig. 4). Positive associations were found between the *r* value of *B. longirostris* and temperature change and between the *r* values of *D. galeata* × *cucullata*, *D. parvula*, and cyclopoid copepods and the population biomass of *D. galeata*.

Fecundity

Multiple-regression models for all taxa significantly explained the variation in the body size adjusted fecundity (Table 2). The amount of variation explained by the models ranged between 46% and 74%. Adjusted fecundity of cladoceran taxa at sampling days was positively related to interpolated biomass estimates of phytoplankton size classes 8 days before these sampling days (Table 2). Positive partial correlations were found between the adjusted fecundity of *D. galeata* and the small size fraction of the phytoplankton community (PHYTSMALL) and between the adjusted fecundity of *B. longirostris* and *D. galeata* × *cucullata* and the large phytoplankton (PHYTLARGE). Furthermore, for each *Daphnia* taxon, significantly negative partial correlations were found between adjusted fecundity on sampling days and interpolated estimates of the population biomass 8 days before these sampling days (Table 2; Fig. 5). The adjusted fecundities of *B. longirostris* and *D. parvula* were also negatively related to the population biomass of *D. galeata*.

Zooplankton versus phytoplankton

No significant associations were found between the total biomass of noncyanobacterial phytoplankton (NONCYAN) and the population biomass of any zooplankton taxon (Table 3). Additional partial correlation analyses indicated that there was a tendency for a negative relationship between *D. galeata* biomass and the large size fraction of algae (PHYTLARGE) (Table 3). Positive partial correlations were found between the biomass of *D. parvula* and small algae (PHYTSMALL) and between cyclopoid copepods and medium-sized algae (PHYTMED).

Discussion

The results of in situ life history and fish exclosure studies have indicated a high impact of planktivorous fish predation on the general size structure of the zooplankton community in Lake Blankaart (Declerck et al. 1997; Declerck 2001). Multiple-regression models that did not take into account

© 2003 NRC Canada

Table 1. Results of partial correlation and multiple-regression analyses on the exponential population growth rate r of cladoceran taxa in Lake Blankaart during 2-week time intervals.

	Partial correlation r_p				
Taxon	r_{BLON} (n = 26)	r_{DGAL} (n = 20)	r_{HYBR} (n = 18)	r_{DPAR} (n = 25)	r_{CYCL} (n = 26)
BLON	–0.79***		–0.55		–0.27
DGAL		–0.54*	0.78**	0.74***	0.65***
HYBR			–0.78**	–0.25	
DPAR	–0.29		–0.39	–0.79***	
CYCL			0.46		–0.63***
ΔTEMP	0.49*	0.45			
PHYTSMALL	–0.26				
PHYTMED			–0.54		
PHYTLARGE	0.29				
Adjusted R^2	0.66***	0.23*	0.63**	0.70***	0.50***

Note: The independent variables were temperature change, biomass of the population, of potential competitors, and of cyclopoid predators, and the biomass of different size fractions of the algae. Adjusted R^2, adjusted coefficient of determination of the multiple-regression model; r_{BLON}, r of *B. longirostris*; r_{DGAL}, r of *D. galeata*; r_{HYBR}, r of *D. galeata* × *cucullata*; r_{DPAR}, r of *D. parvula*; r_{CYCL}, r of cyclopoid copepods; BLON, biomass of *B. longirostris*; DGAL, biomass of *D. galeata*; HYBR, biomass of *D. galeata* × *cucullata*; DPAR, biomass of *D. parvula*; CYCL, biomass of cyclopoid copepods; ΔTEMP, temperature change; PHYTSMALL, biomass of phytoplankton with a greatest axial linear dimension (GALD) smaller than 20 µm; PHYTMED, biomass of phytoplankton with a GALD between 20 and 40 µm; PHYTLARGE, biomass of the phytoplankton with a GALD larger than 40 µm; n, number of observations; blank cells refer to independent variables that were not retained by a forward-selection procedure before the analysis. See the text for more details on the processing of data. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 2. Results of partial correlation and multiple-regression analyses on the residuals of fecundity on adult body length (E) for the cladoceran taxa in Lake Blankaart.

	Partial correlation r_p			
Taxon	E_{BLON} (n = 27)	E_{DGAL} (n = 24)	E_{HYBR} (n = 22)	E_{DPAR} (n = 24)
BLON	–0.32			
DGAL	–0.72***	–0.61**	–0.29	–0.54*
HYBR	–0.28		–0.69***	–0.28
DPAR				–0.65**
CYCP				
TEMP				
PHYTSMALL		0.45*		0.33
PHYTMED	0.32			
PHYTLARGE	0.45*		0.47*	
Adjusted R^2	0.74***	0.46***	0.60***	0.50**

Note: The independent variables were temperature, biomass of the population, of potential competitors, and of cyclopoid predators, and the biomass of different size fractions of the algae 8 days before. Adjusted R^2, adjusted coefficient of determination of the multiple-regression model; E_{BLON}, fecundity of *B. longirostris*; E_{DGAL}, fecundity of *D. galeata*; E_{HYBR}, fecundity of *D. galeata* × *cucullata*; E_{DPAR}, fecundity of *D. parvula*; BLON, population biomass of *B. longirostris*; DGAL, biomass of *D. galeata*; HYBR, biomass of *D. galeata* × *cucullata*; DPAR, biomass of *D. parvula*; CYCL, biomass of cyclopoid copepods; TEMP, temperature; PHYTSMALL, biomass of phytoplankton with a greatest axial linear dimension (GALD) smaller than 20 µm; PHYTMED, biomass of phytoplankton with a GALD between 20 and 40 µm; PHYTLARGE, biomass of the phytoplankton with a GALD larger than 40 µm; n, number of observations; blank cells refer to variables that were not retained by a forward-selection procedure before the analysis. See the text for more details on the processing of data. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

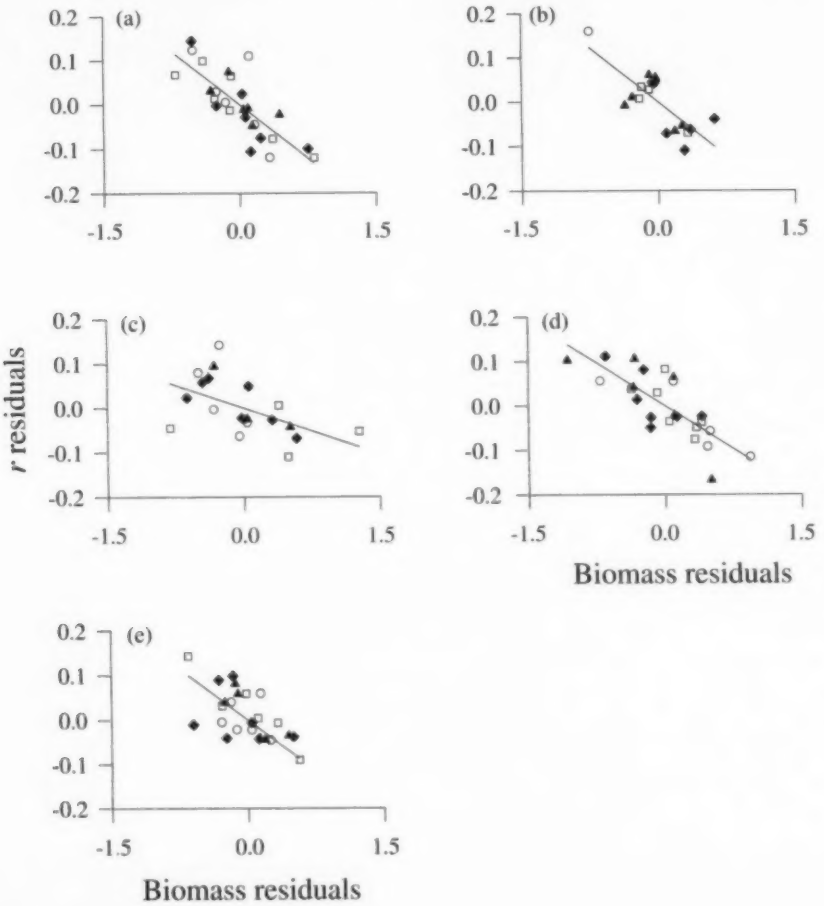
any measure of fish predation intensity could, nevertheless, explain a striking amount of variation in population growth and body size adjusted fecundity of all small- to medium-sized crustacean zooplankton taxa. The amount of explained variation in population growth was considerably lower in *D. galeata* than in the other, smaller cladoceran taxa, consistent with a diminishing impact of fish predation on smaller taxa.

Interactions between zooplankton taxa

The pattern of partial correlations that was found for the adjusted fecundity (Fig. 6) suggests that exploitative competition may to some extent have regulated the dynamics of zooplankton taxa in Lake Blankaart during the study period. There was a negative relationship between the biomass of *D. galeata* and the biomass of the largest size fraction of the algae (PHYTLARGE), suggesting that *D. galeata* may have been able to suppress part of the food sources. Moreover, there was a positive relationship between the adjusted fecundity of *B. longirostris* and *D. galeata* × *cucullata* with the large phytoplankton. Such a pattern may suggest interspecific exploitative competition between *D. galeata* and the populations of *B. longirostris* and *D. galeata* × *cucullata*. How-

© 2003 NRC Canada

Fig. 4. Relations between residuals of the exponential population growth rate r (day^{-1}), estimated for time intervals of ~2 weeks, and of the log(x + 1)-transformed biomass of the population at the start of these intervals for the taxa (*a*) *Bosmina longirostris*, (*b*) *Daphnia galeata* × *cucullata*, (*c*) *D. galeata*, and (*d*) *D. parvula* and for (*e*) cyclopoid copepods in Lake Blankaart during the growing seasons (May–September) of 1994 (open circles), 1995 (open squares), 1996 (solid triangles), and 1997 (solid diamonds). The residuals were obtained by regression of each of both variables on the set of independent variables that were selected by the forward selection procedure.



ever, the results of the partial correlation analyses also indicate that the fecundity dynamics of the zooplankton taxa of Lake Blankaart cannot entirely be understood in terms of interspecific exploitative competition. In each *Daphnia* taxon, adjusted fecundity was negatively correlated with the population biomass of 8 days before, irrespective of phytoplankton biomass. Such negative partial correlations were also observed between the biomass of *D. galeata* and the adjusted fecundity of *Bosmina* and *D. parvula* (Fig. 6).

The population growth rate of *D. galeata* × *cucullata*, *D. parvula*, and cyclopoid copepods were found to show positive partial correlations with the biomass of *D. galeata*, indicating that the population size of these taxa increased when *D. galeata* biomass was high. Possibly, a high biomass of the relatively large *D. galeata* coincides with periods of relatively low fish predation intensity, which may also lead to increased population growth in smaller *Daphnia* taxa. The remaining pattern of significant partial correlations is very analogous to the pattern observed for the adjusted fecundities: in each zooplankton taxon, a substantial amount of the variation in population growth rate during time intervals was explained by the population biomass at the start of these time intervals, irrespective of phytoplankton biomass. In all taxa, these relationships between population growth rate and population biomass were strongly negative.

Several studies have shown that high population densities of Daphnids can decrease the performance of congeners or conspecifics under laboratory conditions. For several *Daphnia* species, negative relationships with the population density of the same species or of other *Daphnia* species have been recorded for traits such as feeding rate (Helgen 1987; Matveev 1993), growth rate (Burns 1995, 2000), fecundity (Matveev 1993; Goser and Ratte 1994; Burns 2000), and mortality (Matveev 1993). In these studies, experimental an-

© 2003 NRC Canada

Fig. 5. Relations between the residuals of fecundity of cladoceran taxa ((*a*) *Bosmina longirostris*, (*b*) *Daphnia galeata* × *cucullata*, (*c*) *D. galeata*, and (*d*) *D. parvula*) in Lake Blankaart determined on sampling days and of the log(x + 1)-transformed interpolated population biomass estimates from 8 days before. The residuals were obtained by regression of each of both variables on the set of the independent variables that were selected by the forward-selection procedure. Open circles, 1994; open squares, 1995; solid triangles, 1996; and solid diamonds, 1997.

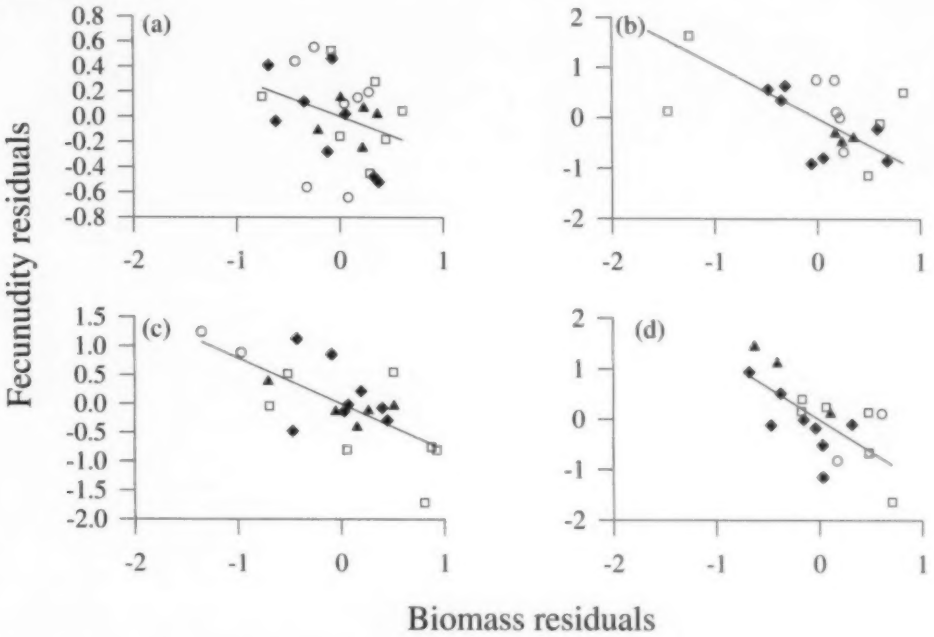


Table 3. Partial correlations (r_p) between the biomass of different size classes of phytoplankton and the biomass of specific zooplankton taxa, controlling for the biomass of other zooplankton taxa or temperature.

	Partial correlation r_p			
	NONCYAN (n = 27)	PHYTSMALL (n = 27)	PHYTMED (n = 27)	PHYTLARGE (n = 27)
BLON	–0.25	–0.32		–0.31
DGAL				–0.53*
HYBR				
DPAR	0.25	0.51*		0.40
CYCL	0.24	–0.23	0.45*	–0.31
TEMP				–0.29
Adjusted R^2	0.16 NS	0.31*	0.17*	0.54***

Note: NONCYAN, biomass of the total noncyanobacterial phytoplankton community; PHYTSMALL, biomass of the phytoplankton with a greatest axial linear dimension (GALD) smaller than 20 µm; PHYTMED, biomass of the phytoplankton with a GALD between 20 and 40 µm; PHYTLARGE, biomass of the phytoplankton with a GALD larger than 40 µm; BLON, population biomass of *B. longirostris*; DGAL, biomass of *D. galeata*; HYBR, biomass of *D. galeata* × *cucullata*; DPAR, biomass of *D. parvula*; CYCL, biomass of cyclopoid copepods; TEMP, temperature; n, number of observations; blank cells refer to variables that were not retained by a forward-selection procedure before the analysis. See the text for more details on the processing of data. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, nonsignificant regression model.

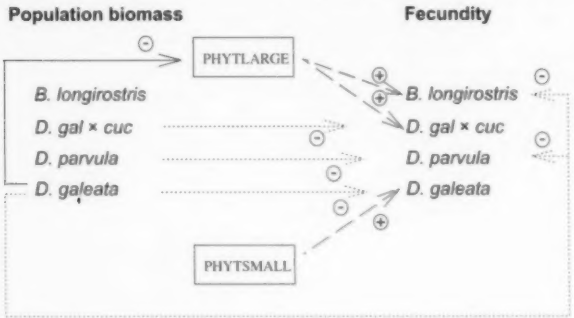
imals were grown under food-satiating conditions, excluding the possibility of food shortage. Matveev (1993) showed that heating of the medium removed the effects, suggesting that a chemical compound mediated the observed interference (allelopathy). Matveev (1993) showed two- to three-fold reductions in the filtering rates and fecundities of *Daphnia* within a range of 1 to 30 *Daphnia* individuals·L^{-1}. During the period of our study, the population densities of *Daphnia* taxa in Lake Blankaart ranged between 2 and 322 individuals·L^{-1}. Chemical interference may therefore have been an important factor affecting the performance of the zooplankton populations.

Intraspecific density dependence

Our results indicate that intraspecific interactions may be important in limiting population growth of small crustacean taxa under food-rich, hypertrophic conditions. For all crustacean taxa, we found a remarkably high degree of intraspecific density dependence that could not be explained by the biomass of phytoplankton size fractions. Despite the rel-

© 2003 NRC Canada

Fig. 6. Pattern of partial correlations between the fecundity of zooplankton taxa, the biomass of phytoplankton size classes, and the biomass of zooplankton taxa observed in Lake Blankaart during the study period (1994–1997). Solid-line arrows indicate the effect of zooplankton grazing on food quantity (only negative relationships presented); broken-line arrows indicate the effect of food quantity on zooplankton fecundity; dotted arrows indicate the effect of zooplankton biomass on zooplankton fecundity, irrespective of food quantity; +, positive interaction; –, negative interaction; PHYTSMALL, size fraction of algae with a greatest axial linear dimension (GALD) less than 20 µm; PHYTLARGE, size fraction of algae with a greatest axial linear dimension larger than 40 µm; *D. gal* × *cuc*, *Daphnia galeata* × *cucullata*.



atively low share of the *Daphnia* populations in the total zooplankton biomass, such intraspecific density dependence was shown in all *Daphnia* taxa for two key population dynamic traits (e.g., body size adjusted fecundity and population growth). *Bosmina* also had a strong negative impact on its population growth, and although this taxon reached very high population biomasses, it was not found to affect any of the three *Daphnia* taxa. Several mechanisms could be responsible for the high intraspecificity of the density dependence.

The inappropriate assessment of food availability

It could be argued that the importance of intraspecific exploitative competition was underestimated in our study to the extent that the investigated taxa rely on specific diets of which depletion by selective grazing could not be detected by our assessment of food availability. In such a case, population biomass could have been a better correlate of food availability than our measures of phytoplankton biomass. This may certainly have been the case for the cyclopoid copepods. *Acanthocyclops robustus*, the dominating cyclopoid copepod in Lake Blankaart, is a selective feeder that may feed on phytoplankton, rotifers, ciliates, heterotrophic nanoflagellates, and small crustaceans (Gliwicz and Umana 1994). As some of these potential food sources were not quantified in our study, the importance of exploitative competition for cyclopoids could not be assessed. Several studies have also indicated that *Bosmina* may feed selectively, because of a dual-option feeding mode (DeMott 1982; Bleiwas and Stokes 1985), and are able to discriminate between food particles by taste (DeMott 1986). However, it is improbable that the intraspecific effects of biomass on adjusted fecundity and population growth in the *Daphnia* populations were due to exploitative competition, as food selectivity in *Daphnia* is low (DeMott 1982; Bleiwas and Stokes 1985; Kerfoot et al. 1985) and the overlap between the food niches of *Daphnia* species is high (Kerfoot et al. 1985; Lampert 1987), whereas in this study, negative intraspecific interactions were more pronounced and numerous than negative interspecific interactions.

Cannibalism

A negative relationship between the biomass of a population and the growth of this population may be the result of strong cannibalism. With the exception of cyclopoid copepods, however, no cannibalistic taxa were involved in our study.

Switching prey selectivity by predators

If the selectivity of a predator for a prey type depends on its relative frequency, the per capita probability for a prey of being eaten may increase with increasing density of its population (Gatto 1991). Two types of predators, i.e., cyclopoid copepods and fishes, potentially prey upon the cladoceran populations in Lake Blankaart. If density-dependent prey selection of cyclopoid copepods was the regulating factor of the dynamics of prey taxa, negative relationships between cyclopoid and overall prey abundance should have been observed as well. In the case of fish predation, the demographic impact of density-dependent prey selection by fishes should have been most pronounced in the largest taxa, given the size-selective feeding mode of fish. However, the density dependence of population growth tended to be stronger in the smaller zooplankton taxa (*B. longirostris*, *D. parvula*, *D. galeata* × *cucullata*) than in *D. galeata*, the largest taxon. Another argument against density dependence mediated by predation is that such predation cannot account for the observed density dependence in fecundity. Although copepods may forage on eggs in the brood pouch and decrease the number of eggs at a given body size, they can only do so in large cladocerans and not in small *Daphnia* species (Gliwicz and Lampert 1994). Although size-selective fish predation may lead to a decrease in fecundity for a given body size, this should be more pronounced in the larger taxa, given the size selectivity of fish predation.

Intraspecific chemical interference

Intraspecific chemical interference can be very strong. In medium preconditioned by *D. carinata*, Matveev (1993) showed a reduction in the filtering rate of *D. carinata* that was four times stronger than the reduction observed in another *Daphnia* species. Reduced food uptake rates may lead to reductions in fecundity and population growth rate.

Life-strategy shifts by intraspecific interaction (LiSSII)

Zooplankton can undergo chemically mediated shifts in life strategy when grown at high densities of conspecifics (LiSSII; Cleuvers et al. 1997). In anticipation of periods with low food availability, such shifts consist of changes in the pattern of energy allocation, with reductions in offspring quantity (e.g., fecundity) but increases in their quality (e.g., higher dry weight, body lipid content, and resistance to starvation). LiSSII responses may also affect the dynamics of populations as reduced fecundities imply reduced population growth rates.

© 2003 NRC Canada

As described above and given the high population maxima reached by the zooplankton taxa in Lake Blankaart during the study period, both intraspecific chemical interference and LiSSIIs seem to be the most plausible mechanisms responsible for the high degree of intraspecific density dependence observed in our study. The accumulating evidence of chemical interactions between cladocera as provided by laboratory experiments (Goser and Ratte 1994; Cleuvers et al. 1997; Burns 2000) strongly suggests that chemical communication may be important in determining the dynamics and structure of zooplankton populations or even entire zooplankton communities. Burns (2000), for example, found a tendency for a higher sensitivity to allelopathic effects in small vs. larger zooplankton taxa. She suggested that chemical interference could be an additional mechanism explaining the apparent competitive superiority of large zooplankton to small zooplankton, as proposed by the size efficiency hypothesis (Brooks and Dodson 1965). With the exception of Seitz (1980) and Matveev (1991), however, the potential role of chemical interference in field populations has seldom been recognised.

The strong intraspecific density dependence observed in most zooplankton taxa of our study suggests that, under hypertrophic conditions, intraspecific chemical interactions may be important mechanisms that set limits to the population growth of small zooplankton taxa. One important conceptual implication may be that, under such conditions, a kind of "lateral" control of populations may form an alternative to the classical views of top-down vs. bottom-up control. It may also cast another light on the co-existence of species. The discussion on what factors facilitate the co-existence of species has long been dominated by two views (Tokeshi 1999). Species are assumed to co-exist (*i*) because they are able to avoid competition by niche segregation or (*ii*) because their relative competitive abilities are frequently modified by environmental disturbances, preventing competitive exclusion. "Self-regulation" by intraspecific chemical interactions in taxa that are superior in the competition for food may form an alternative mechanism that promotes the co-existence of species, as it may relax the strength of exploitative competition. In addition, it may also provide a mechanism to explain why populations are not necessarily destabilized by an increase in their resources (e.g., "paradox of enrichment"; Kirk 1998).

Methodological implications

Our results indicate that care should be taken with the interpretation of correlations between population size and fecundity in zooplankton populations. Based on experiments and descriptive field studies, Matveev (1983) proposed that negative correlations between fecundity and population density are indicative of intra- and inter-specific exploitative interactions, if appropriate time lags were taken into account. Since then, several studies have used this approach to document exploitative competition between zooplankton taxa in natural zooplankton communities (Matveev 1983; Bengtsson 1993; Boersma 1995), potentially overlooking the impact of intra- and inter-specific chemical interactions. Despite the problems related to the assessment of food availability in eutrophic systems (Boersma and Vijverberg 1994; Müller-Navarra and Lampert 1996), we believe that when making inferences about competitive interactions in field populations, correlation analyses should always be combined with information on food availability. Moreover, knowledge about the feeding niche of the organisms under study should be taken into account.

Acknowledgements

We thank Stanley Dodson and Karl Cottenie for valuable comments on a previous version of this manuscript. A scholarship was provided to S.D. by the Flemish Institute for the stimulation of Scientific and Technological Research in the Industry (I.W.T.). We also thank Natuurrpunt for the permission to work in the nature reserve "De Blankaart".

References

Achenbach, L., and Lampert, W. 1997. Effects of elevated temperatures on threshold food concentrations and possible competitive abilities of differently sized cladoceran species. Oikos, **79**: 469–476.

Bengtsson, J. 1993. Interspecific competition and determinants of extinction in experimental populations of 3 rockpool *Daphnia* species. Oikos, **67**: 451–464.

Bleiwas, A.H., and Stokes, P.M. 1985. Collection of large and small food particles by *Bosmina*. Limnol. Oceanogr. **30**: 1090–1092.

Boersma, M. 1995. Competition in natural populations of *Daphnia*. Oecologia, **103**: 309–318.

Boersma, M., and Vijverberg, J. 1994. Seasonal variations in the condition of two *Daphnia* species and their hybrid in a eutrophic lake: evidence for food limitation under field conditions. J. Plankton Res. **16**: 1793–1809.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., and Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. **24**: 419–456.

Brooks, J.H., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science (Wash., D.C.), **150**: 28–35.

Burns, C.W. 1995. Effects of crowding and different food levels on growth and reproductive investment of *Daphnia*. Oecologia, **101**: 234–244.

Burns, C.W. 2000. Crowding-induced changes in growth, reproduction and morphology of *Daphnia*. Freshw. Biol. **43**: 19–29.

Cleuvers, M., Goser, B., and Ratte, H.T. 1997. Life-history shift by intra-specific interaction in *Daphnia magna*: change in reproduction from quantity to quality. Oecologia, **110**: 337–345.

Declerck, S. 2001. An ecological and ecological-genetic study of *Daphnia* in a shallow hypertrophic lake. Ph.D. thesis, University of Gent, Gent, Belgium.

Declerck, S., De Meester, L., Podoor, N., and Conde Porcuna, J.M. 1997. The relevance of size efficiency to biomanipulation theory: a field test under hypertrophic conditions. Hydrobiologia, **360**: 265–275.

DeMott, W.R. 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. Limnol. Oceanogr. **27**: 518–527.

DeMott, W.R. 1986. The role of taste in food selection by freshwater zooplankton. Oecologia, **69**: 334–340.

Flössner, D., and Kraus, K. 1986. On the taxonomy of the *Daphnia hyalina–galeata* complex (Crustacea: Cladocera). Hydrobiologia, **137**: 97–115.

Gatto, M. 1991. Some remarks on models of plankton densities in lakes. Am. Nat. **137**: 264–267.

© 2003 NRC Canada

Gliwicz, Z.M. 1990. Food thresholds and body size in cladocerans. Nature (Lond.), **343**: 638–640.

Gliwicz, Z.M., and Lampert, W. 1994. Clutch-size variability in *Daphnia*: body-size related effects of egg predation by cyclopoid copepods. Limnol. Oceanogr. **39**: 479–485.

Gliwicz, Z.M., and Umana, G. 1994. Cladoceran body size and vulnerability to copepod predation. Limnol. Oceanogr. **39**: 419–424.

Goser, B, and Ratte, H.T. 1994. Experimental evidence of negative interference in *Daphnia magna*. Oecologia, **98**: 354–361.

Helgen, J.C. 1987. Feeding rate inhibition in crowded *Daphnia pulex*. Hydrobiologia, **154**: 113–119.

Hessen, D.O., Faafeng, B.A., and Andersen, T. 1995. Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. Can. J. Fish. Aquat. Sci. **52**: 733–742.

Hough, R.A., Fornwall, M.D., Negele, B.J., Thompson, R.L., and Putt, D.A. 1989. Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication. Hydrobiologia, **173**: 199–217.

Jeppesen, E., Jensen, J.P., Søndergaart, M., Lauridsen, T., and Landkildehus, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a nutrient gradient. Freshw. Biol. **45**: 201–218.

Kerfoot, C., Arbor, A., DeMott, W., and DeAngelis, D.L. 1985. Interactions among cladocerans: food limitation and exploitative competition. Arch. Hydrobiol. Beih. Ergebn. Limnol. **21**: 431–451.

Kirk, K.L. 1998. Enrichment can stabilize population dynamics: autotoxins and density dependence. Ecology, **79**: 2456–2462.

Lampert, W. 1978. A field study on the dependence of the fecundity of *Daphnia* spec. on food concentration. Oecologia, **39**: 363–369.

Lampert, W. 1987. Feeding and nutrition in *Daphnia*. *In* Daphnia. *Edited by* R.H. Peters and R. De Bernardi. Mem. Ist. Ital. Idrobiol., Pallanza, Italy.

Matveev, V. 1983. Estimating competition in cladocerans using data on dynamics of clutch size and population density. Int. Rev. Gesamten. Hydrobiol. **68**: 785–798.

Matveev, V. 1985. Delayed density dependence and competitive ability in two cladocerans. Arch. Hydrobiol. Beih. Ergebn. Limnol. **21**: 453–459.

Matveev, V. 1991. Exploitative and interference competition among planktonic crustaceans in a subtropical lake. Arch. Hydrobiol. **123**: 53–68.

Matveev, V. 1993. An investigation of allelopathic effects of *Daphnia*. Freshw. Biol. **29**: 99–105.

Moss, B., Kornijow, R., and Measey, G.J. 1998. The effects of nymphaeid (*Nuphar lutea*) density and predation by perch (*Perca fluviatilis*) on the zooplankton communities in a shallow lake. Freshw. Biol. **39**: 689–697.

Müller-Navarra, D., and Lampert, W. 1996. Seasonal patterns of food limitation in *Daphnia galeata*: separating food quantity and food quality effects. J. Plankton Res. **18**: 1137–1157.

Persson, L., Andersson, G., Hamrin, S.F., and Johansson, L. 1988. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. *In* Complex interactions in lake communities. *Edited by* S.R. Carpenter. Springer, New York.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225.

Seitz, A. 1980. The coexistence of three species of *Daphnia* in the Klostersee. I. Field studies on the dynamics of reproduction. Oecologia, **45**: 117–130.

Sluzarczyk, M. 1997. Impact of fish predation on a small-bodied cladoceran: limitation or stimulation? Hydrobiologia, **342/343**: 215–221.

Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. Blackwell Science, Oxford.

© 2003 NRC Canada

Energy losses due to routine and feeding metabolism in young-of-the-year juvenile Atlantic cod (*Gadus morhua*)

Myron A. Peck, Lawrence J. Buckley, and David A. Bengtson

Abstract: We examined the effects of body size (3–13 cm total length) and temperature (4.5, 8.0, 12.0, and 15.5 °C) on routine (R_R) and feeding (R_{SDA}) energy losses by laboratory-reared, young-of-year juvenile Atlantic cod (*Gadus morhua*). The magnitude of the effect of temperature on R_R, expressed via the Q_{10}, was nonlinear. Q_{10} values were greatest at temperatures between 4.5 and 8.0 °C and were lowest between 8.0 and 15.5 °C, with larger fish tending to exhibit the greatest change in R_R irrespective of the temperature combination. Energy losses resulting from R_{SDA} were ~4% of consumed energy, a value less than half that estimated for larger, year-1+ juvenile cod fed similar-sized rations. Data from this and other studies were combined to generate an equation estimating routine energy loss at different temperatures and body sizes for cod. The equation describes R_R over the eight orders of magnitude difference in body size from young larvae to adults within a range of environmental temperatures experienced by this species on Georges Bank and other areas in the North Atlantic.

Résumé : Nous avons étudié les effets de la taille (3–13 cm de longueur totale) et de la température (4,5, 8,0, 12,0 et 15,5 °C) sur les pertes d'énergie de routine (R_R) et d'alimentation (R_{SDA}) chez des jeunes morues franches (*Gadus morhua*) de l'année, élevées en laboratoire. L'importance de l'effet de la température sur R_R, exprimée par le Q_{10}, n'est pas linéaire. Les valeurs de Q_{10} sont maximales aux températures entre 4,5 et 8,0 °C et minimales entre 8,0 et 15,5 °C et les plus gros poissons subissent les plus forts changements de R_R, quelle que soit la combinaison de températures. Les pertes d'énergie dues à R_{SDA} représentent ~4 % de l'énergie consommée, soit moins de la moitié de la valeur estimée chez des jeunes morues d'âge 1+ nourries de rations semblables. Les données de notre étude combinées à celles d'autres travaux ont permis de produire une équation pour estimer les pertes d'énergie de routine à différentes températures et pour différentes tailles chez la morue. L'équation décrit R_R pour des différences de tailles de l'ordre de 10^8, allant des jeunes larves aux adultes, sur la gamme des températures du milieu rencontrées par cette espèce sur le banc Georges et les autres régions de l'Atlantique Nord.

[Traduit par la Rédaction]

Introduction

Field data collected for cod (*Gadus morhua*) in the Northwest Atlantic suggest that factors operating during the first year of life, when these fish undergo a protracted transition from the pelagic to a benthic habitat at ~3–7 cm total length (TL) (Lough and Potter 1993), influence year-class success in some years (Campana et al. 1989; Campana 1996). However, in the decades of research on this species, the year-0 juvenile period (3 to ~13 cm TL) has received relatively little attention because of difficulties in both the successful rearing of juvenile gadids in the laboratory and the live capture and transport from the wild. Recent advances in the aquaculture of Atlantic cod now permit us to bridge the gap between physiological studies conducted on larvae (<2 cm TL) and those conducted on larger demersal juveniles (>25 cm TL) and adults.

The rate of respiration, measured in terms of O_2 consumption, has been commonly used as a proxy for metabolic rate in aquatic and terrestrial animals (Fry 1957; Brett and Groves 1979). Rates of O_2 consumption by fish have been classified into different levels based on the activity occurring during the measurements. These levels include standard (R_S), routine (R_R), specific dynamic action (R_{SDA}), and active (R_A) respiration rates corresponding to energy losses resulting from basal metabolism (e.g., anaesthetized fish), routine movements,

Received 23 November 2002. Accepted 16 April 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 9 September 2003.
J17200

M.A. Peck.[1,2] Graduate School of Oceanography, University of Rhode Island, South Ferry Rd., Narragansett, RI 02882, U.S.A.
L.J. Buckley. URI/NOAA CMER Program, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, U.S.A.
D.A. Bengtson. Department of Fisheries, Animal and Veterinary Science, University of Rhode Island, Kingston, RI 02881, U.S.A.

[1]Corresponding author (e-mail: myron.peck@uni-hamburg.de).

[2]Present address: Institute for Hydrobiology and Fisheries Research, University of Hamburg, Olbersweg 24, D-22767 Hamburg, Germany.

 doi: 10.1139/F03-079 © 2003 NRC Canada

digestion and assimilation of food, and active swimming, respectively (Fry 1957; Brett and Groves 1979). The increase in rates of O_2 consumption during feeding (R_{SDA}) has also been termed "apparent heat increment" (e.g., Blaikie and Kerr 1996).

The energy losses owing to metabolism may be estimated from respiratory data previously collected on cod larvae (e.g., Laurence 1978; Hunt von Herbing and Boutilier 1996), large juveniles (e.g., Soofiani and Hawkins 1982; Schurmann and Steffensen 1997), and adults (e.g., Saunders 1963; Blaikie and Kerr 1996). These and other studies on cod have quantified the principal factors affecting rates of metabolism in fish: water temperature, body size, feeding, and activity level. Comparable respiratory data at different temperatures for year-0 juvenile Atlantic cod are lacking. Consequently, bioenergetic models similar to those created for adult cod (e.g., Hansson et al. 1996) and those used in larval cod individual-based models (IBMs) (e.g., Werner et al. 1996; Hinrichsen et al. 2002) have not been developed for year-0 juveniles. Application of bioenergetic models and (or) extension of larval IBMs to year-0 juveniles should permit a better understanding of the factors affecting year-class success in this species.

The objective of the present research was to quantify the effects of temperature and body size on energy losses resulting from R_R and R_{SDA} respiration by young juvenile Atlantic cod. Measurements were taken over a range in body sizes (3–13 cm TL) at each of four temperatures (4.5, 8.0, 12.0, and 15.5 °C). The range in body sizes studied corresponded to the pelagic, presettlement period in May–June through the postsettlement period in September–October on Georges Bank in the Northwest Atlantic. The range in temperatures encompassed those experienced by young-of-year cod on Georges Bank. The rates of routine and feeding metabolism measured in this study were compared with those measured in previous studies using larval, larger juvenile, and adult cod to construct a more complete picture of the metabolic ontogeny of this species.

Materials and methods

Juvenile cod husbandry

Several batches of juvenile Atlantic cod (2 to 3 months old, 2–3 cm TL) were obtained from an aquaculture research center (University of Maine, Orono, Maine), transported to the National Oceanic and Atmospheric Administration – National Marine Fisheries Service (NOAA/NMFS) Narragansett Laboratory (Narragansett, Rhode Island), and maintained separately. Juveniles in these batches were the progeny of wild-caught adult broodstock (Gulf of Maine – Great South Channel fish) induced by photothermal cues to spawn in captivity at the NOAA/ NMFS Narragansett Laboratory. Once transported to the laboratory, the juveniles were held in temperature-controlled, flow-through, circular tanks (91.4 cm and 121.9 cm diameter) receiving filtered (20 μm) Narragansett Bay seawater (1–3 L·min^{-1}). The salinity was 29–32‰, and light levels were 0.2–1.0 μE (μmols·m^{-2}·s^{-1}). Fish were fed an artificial diet (BioKyowa™, pellet sizes 0.5, 1, or 2 mm; BioKyowa Inc., Cape Girardeau, MO 63702-1550, U.S.A.) one to three times daily depending on fish size.

Metabolic measurements

The energy loss resulting from juvenile cod metabolism was estimated using a 12-chamber, flow-through respirometer modified from the design of Ross and McKinney (1988). Juvenile cod were held individually or in a group within opaque plastic chambers (with clear acrylic tops) submerged in a temperature-controlled (±0.3 °C), recirculating water bath. Water continually flowed through each chamber to waste and was redirected sequentially past an oxygen microelectrode (MI-730; Microelectrodes Inc., Bedford, N.H.) and a flow gauge in 3- to 5-min intervals by the sequential operation of parallel air-piston valves. With 12 chambers operating, measurements were made on each chamber every hour. A computer controlled the valve operation and collected data from the microelectrode and flow gauge. Temperatures were measured every hour (Optic Stowaway; Onset Corp., Bourne, Mass.). Data from micro-Winkler dissolved oxygen titrations were collected at the beginning, middle, and end of each trial and used to convert the microelectrode output (mV) to oxygen concentration (mg O_2·L^{-1}). The [O_2] in each chamber was maintained between 80% and 95% of saturation using seawater flow rates between 1.2 and 3.5 L·h^{-1}. Two chamber sizes (0.5 and 1.5 L) were used, and chamber size increased with fish size to allow routine movements by fish of 3–13 cm TL. The number of fish within each chamber depended on fish size and temperature, and when a group was used (at low temperatures and (or) small fish sizes), fish were of similar size (weight coefficient of variation ~14%). Chambers were shielded from laboratory stimuli (movements and noise), and a video camera allowed the fish to be viewed without being disturbed. Salinity was between 30 and 32‰, and the light level was 1.5 μE during a 14-h photoperiod (0600–2000 hours, instantaneously on and off).

Trials were conducted at each of four temperatures (4.5, 8.0, 12.0, and 15.5 °C) using fish of different mean sizes as the fish grew over the course of about 8 months (from ~3 to 13 cm TL) in the lab (Table 1). Each trial lasted 5 days during which O_2 consumption by fish was measured in 0.5- to 1.0-h intervals during nonfeeding and feeding periods (Fig. 1). During a trial, 4–12 chambers were run simultaneously (3–11 with fish and one without fish (the control chamber)). Fish were acclimated to the test temperature at a rate of 1 °C·day^{-1} and remained at this temperature for 7–14 days before the trial. On day 1, unfed (for 1 day) cod were introduced into chambers and acclimated overnight. Fish remained unfed within the chambers on day 2 and were fed once on day 3 and once on day 4 (BioKyowa™; 1-mm pellet, feedings between 1100 and 1500 hours). Fish were not fed to satiation, but received smaller rations that were above their maintenance (zero-growth) requirements. Maintenance requirements were previously determined for similar-sized juveniles held at the same temperatures and provided the same diet (Peck et al. 2003). Fish were removed from the chambers on day 5, and the length (standard length (SL) and TL, ±0.01 cm, dial caliper) and weight (wet (WW) and dry (DW), ±0.0001 g, Mettler Microbalance; Mettler-Toledo Inc., Columbus, OH 43240, U.S.A.) of each fish were measured (DW was determined after drying in an oven at 60 °C for >48 h). Fish ash weight (AW) was determined for randomly selected individuals by burning at 500 °C for 12 h.

The respiration rate (mg O_2·fish^{-1}·h^{-1}) was equal to

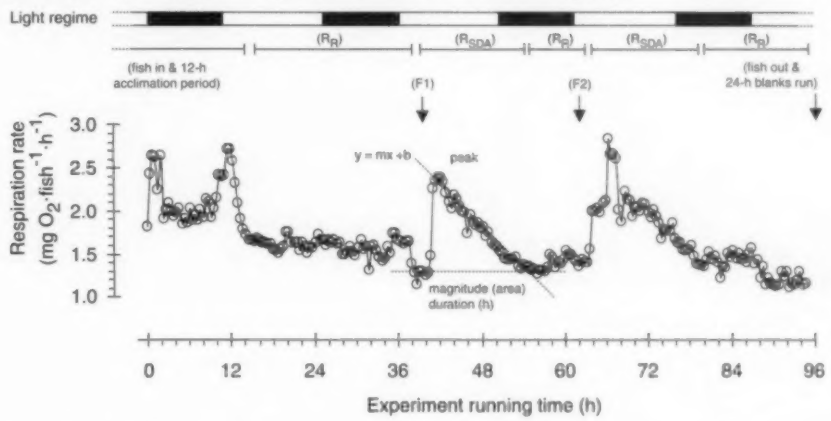
© 2003 NRC Canada

Table 1. Summary data for respirometry trials using young juvenile cod (*Gadus morhua*).

Trial	Chambers (*N*)	Temperature mean ± range (°C)	Fish in chamber (*N*)	Age (dph)	DW range (g)	SL range (cm)
1	4	4.5±0.4	11–15	95	0.019–0.059	NM
2	9	4.6±0.2	2–3	151	0.310–0.695	5.66–9.33
3	10	4.0±0.3	2–4	274	0.814–2.447	7.75–10.98
4	7	7.5±0.2	8–14	110	0.048–1.280	3.29–4.20
5	8	8.1±0.2	3–6	123	0.116–0.233	3.93–4.77
6	5	7.8±0.3	1	193	1.364–1.957	9.38–9.95
7	6	7.9±0.4	1–3	223	0.642–2.476	7.40–11.13
8	5	11.9±0.3	6–9	92	0.025–0.081	2.34–3.66
9	8	11.9±0.2	2–4	131	0.220–0.841	5.05–7.55
10	8	12.2±0.3	2–3	145	1.270–2.201	3.93–5.36
11	9	12.4±0.5	2–3	306	2.699–4.852	7.99–10.83
12	7	15.3±0.2	4–7	110	0.056–0.161	3.20–4.49
13	8	15.0±0.2	2–4	137	0.183–0.431	4.68–6.17
14	11	15.4±0.5	1	161	1.813–5.438	10.05–12.16
15	8	15.7±0.4	1	167	1.291–3.299	8.57–10.67
16	10	15.5±0.3	2	291	1.628–2.505	9.25–10.61

Note: The range in the mean fish dry weights (DW) and standard lengths (SL) in each trial are provided. Fish age is expressed in days posthatch (dph). Sizes and ages were determined at the end of each 5-day trial. NM, not measured.

Fig. 1. Protocol used and example of data collected during respiration trials measuring routine (R_R) and feeding (R_{SDA}) respiration (O_2 consumption) in young-of-year juvenile cod (*Gadus morhua*). Data are shown for one juvenile (2.5 g dry weight (DW), 11.2 cm total length (TL)) at 15.5 °C. Feeding times (*F*1 and *F*2) are indicated. The peak, duration, and magnitude of R_{SDA} were determined for both feeding periods: $R_{SDA\ PEAK}$ was measured relative to the mean of R_R measurements obtained 4–6 h immediately before feeding, and $R_{SDA\ DUR}$ was determined from linear regression of the decrease after feeding. Increased R_R during the acclimation period and changes associated with the diel cycle (e.g., 8–12 h) were absent in the measurement period.



$$(1) \qquad R = V_W[O_{2c} - O_{2f} + \tau(dO_{2f}\cdot dt^{-1})]N^{-1}$$

where O_{2c} and O_{2f} represent $[O_2]$ ($mg\cdot L^{-1}$) in the control chamber (c) and a chamber with fish (f), respectively, V_w represents flow rate ($L\cdot h^{-1}$), and N represents the number of fish in the chamber. A derivative, or storage term, correction is included in eq. 1, where τ (flushing time (h)) = (chamber volume (L))$\cdot V_W^{-1}$ and $dO_{2f}\cdot dt^{-1}$ is the rate of change in $[O_2]$ with time (t) (Northby 1976). Weight-specific rates were determined from eq. 1 by substituting DW (total in chamber) for N. The energy loss resulting from R_R was calculated as the mean value of measurements taken during unfed portions of each trial (Fig. 1). The effect of temperature on juvenile cod R_R was described via calculation of the Q_{10}, which normalizes the change in metabolic rate at two different temperatures to that produced by a 10 °C increase in temperature:

$$(2) \qquad Q_{10} = (R_{R2}/R_{R1})^{10/(T2-T1)}$$

where $T1$ and $T2$ correspond to lower and higher temperatures, respectively.

Energy loss as a result of R_{SDA} was estimated from the increase in the O_2 consumption rate after each of the two feedings (days 2 and 3). The peak rate ($R_{SDA\ PEAK}$), duration ($R_{SDA\ DUR}$), and magnitude ($R_{SDA\ MAG}$) of R_{SDA} were measured (Fig. 1). $R_{SDA\ PEAK}$ was equal to the highest rate of O_2 consumption, usually measured shortly after feeding. $R_{SDA\ DUR}$ was equal to the time (h) required for O_2 consumption rates

© 2003 NRC Canada

to decrease to the mean rate of measurements taken 4–6 h immediately before feeding. Durations were calculated from linear regressions of the postfeeding decrease in O_2 consumption rate and time. $R_{SDA\ MAG}$ (J·fish^{-1}) was estimated by integration (Fig. 1) and expressed as a percentage (%) of the consumed food energy (J·fish^{-1}). The mean (± standard error (SE)) energy content of the food was 20.82 (0.31) J·mg DW^{-1} (n = 15; Gentry Phillipson Micro-bomb calorimeter; Gentry Instruments Inc., Aiken, SC 29804, U.S.A.). The BioKyowa diet was 55% protein, 10% fat, 4% fiber, and 17% ash (manufacturer's data).

Data collected in this study were analyzed by linear and multiple linear regression analyses and analysis of covariance using SAS (SAS 1989). Parameter estimates were obtained by the least-squares method, and data were log transformed when required. Significance was determined at the $\alpha = 0.05$ level.

Literature values for cod R_R were taken directly from published tables or figures. Data from figures were collected after digitization of the images (MATLAB 5.3; Mathworks Inc., Natick, Mass.; DIGIREAD shareware). All O_2 consumption rate and fish weight data from literature sources were converted to per fish rates (mg O_2·fish^{-1}·h^{-1}) and dry weight (DW), respectively. The following conversion factors were used: DW = 0.217WW – 0.040 (this study); 1 µL O_2 = 1.428 µg O_2 (Green and Carritt 1967); 1 mg O_2 = 3.25 cal (Brett and Groves 1979); 1 cal = 4.184 J.

Results

General

A total of 16 trials were conducted using Atlantic cod ranging in sizes and ages from 2.34–12.16 cm SL (0.019 to 5.438 g DW) and 92–306 days after hatch, respectively (Table 1). The length (cm) and weight (g) of juvenile cod (fish used in this study and siblings collected from rearing tanks) were significantly related ($p < 0.0001$) based on the following equations:

(3) $\mathrm{TL} = 1.086(\mathrm{SL}) - 0.013, \quad n = 470,\ R^2 = 0.999$

(4) $\mathrm{SL} = 4.833(\mathrm{WW})^{0.323}, \quad n = 524,\ R^2 = 0.996$

(5) $\mathrm{SL} = 8.098(\mathrm{DW})^{0.312}, \quad n = 384,\ R^2 = 0.991$

(6) $\mathrm{DW} = 0.217(\mathrm{WW}) - 0.040, \quad n = 360,\ R^2 = 0.993$

(7) $\mathrm{AW} = 0.160(\mathrm{DW}) - 0.006, \quad n = 50,\ R^2 = 0.974$

Routine metabolism

No clear diel patterns were observed in juvenile cod routine respiration rates (R_R). Elevated patterns in R_R, which occurred during portions of the acclimation period (e.g., 10–13 h; Fig. 1), were absent during the measurement period (e.g., 34–36, 59–62, and 86–88 h; Fig. 1). The rates of energy loss resulting from R_R increased proportionally to the logarithm of DW by factors of 0.678, 0.728, 0.746, and 0.761 at water temperatures of 4.5, 8.0, 12.0, and 15.5 °C, respectively (Fig. 2*a*; Table 2). The trend of increasing slope with increasing temperature was not significant at the 0.05 level (analysis of covariance, $F = 2.36$, $p = 0.075$), and a multiple linear regression could be used to describe the combined effects of T and body size (DW) on the mean rate of R_R:

(8) $R_R = 0.398(\mathrm{DW})^{0.731}\exp^{(T\cdot 0.076)}, \quad n = 123,\ R^2 = 0.978$

where R_R is measured in mg O_2·fish^{-1}·h^{-1}. The associated loss of energy in J·fish^{-1}·h^{-1} can be calculated by substituting a value of 5.414 for 0.398 in eq. 8.

The mean rates of R_R of relatively small, medium, and large juveniles increased exponentially with temperature (Fig. 2*b*). Q_{10} values calculated using eq. 2 for size-specific R_R estimates at different temperature combinations (equations in Table 2) were between 1.35 and 3.28. The exponential temperature term in eq. 8 (0.076) indicated a mean Q_{10} of 2.14 for all body sizes and temperatures.

Feeding metabolism

The mean (± standard deviation (SD)) $R_{SDA\ PEAK}$ was 1.54 (0.20) times greater than the mean routine rate before feeding (Fig. 3*a*) and was not significantly correlated to ration size, but decreased slightly with T:

(9) $R_{SDA\ PEAK} = 1.75 - 0.02(T), \quad n = 166,\ R^2 = 0.08,\ p < 0.001$

Temperature was not significantly correlated with $R_{SDA\ DUR}$ over the range in ration sizes used in this study (e.g., consumption of a 0.65% WW ration yielded mean (±SD) $R_{SDA\ DUR}$ of 5.5 (0.9), 6.7 (1.7), 6.6 (1.6), and 6.5 (2.1) h at 4.5, 8.0, 12.0, and 15.5 °C, respectively). $R_{SDA\ DUR}$ ranged from 2.9 to 13.2 h and increased with the amount of food consumed (F) (Fig. 3*b*) as

(10) $R_{SDA\ DUR} = 7.27(F)^{0.339}, \quad n = 166,\ R^2 = 0.33,\ p < 0.001$

The $R_{SDA\ MAG}$, expressed as a percentage (%) of the consumed food energy, was best described using a multiple linear regression:

(11) $R_{SDA\ MAG} = 0.80(T)^{0.527}(F)^{-0.664}(\mathrm{WW})^{-0.139}, \quad n = 166,\ R^2 = 0.47,\ p < 0.001$

where the value ranges of independent variables were as follows: T = 4.5–15.5 °C, F (food ration size) = 0.3–3.2% WW, and WW = 0.15–23.01 g. A stepwise multiple linear regression (Max R^2; SAS 1989) indicated that one variable, F, explained 28% of the variability, whereas the best two-parameter model ($F + T$) explained 40% of the variability in the percentage of food energy lost via R_{SDA}. The mean (±SE) percentage of consumed food energy lost to R_{SDA} was 3.9% (0.1) (n = 166).

Discussion

Routine energy loss and body size

The present study includes estimates of routine energy losses in young-of-year juvenile cod that bridge the gap between studies performed on larvae and those performed on larger juveniles and adults. Studies comparing the respiratory physiology of large juvenile and adult Atlantic cod often use a factor of 0.82 to adjust rates resulting from body

© 2003 NRC Canada

Fig. 2. Rates of routine respiration (R_R) at 4.5 °C (diamonds), 8.0 °C (squares), 12.0 °C (triangles), and 15.5 °C (circles) for year-0 juvenile Atlantic cod (*Gadus morhua*). (*a*) R_R versus body size (dry weight (DW)); each datum is the mean respiration rate and mean dry weight of similar-sized fish (n = 1 to 15) in an individual chamber. Regression statistics are provided in Table 2. (*b*) R_R versus temperature (T) for 0.040 g DW fish ($R_R = 0.047\exp^{0.084T}$, $R^2 = 0.98$), 0.360 g DW fish ($R_R = 0.207\exp^{0.062T}$, $R^2 = 0.91$), and 2.190 g DW fish ($R_R = 0.523\exp^{0.103T}$, $R^2 = 0.98$). Each datum is the mean R_R of fish in 5 to 6 chambers.

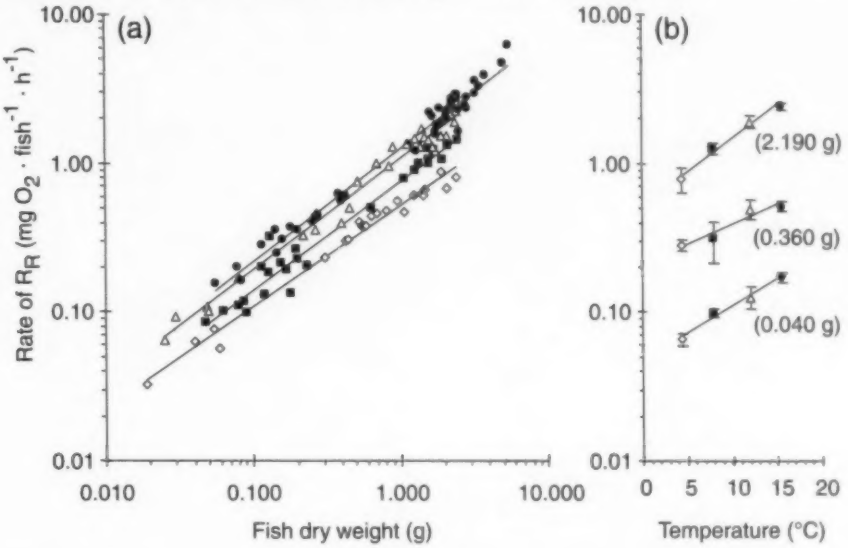


Table 2. Parameter estimates for equations relating the mean rate of routine respiration (R_R) of young-of-the-year juvenile cod (*Gadus morhua*) to mean body size (dry weight (DW)) at each of four temperatures.

		$\log_{10}R_R = \log_{10}a + b\cdot\log_{10}$DW			
T (°C)	DW range (g)*	a mean (±SE)	b mean (±SE)	n	R^2
4.5	0.0192–2.4473	–0.287 (0.013)	0.678 (0.021)	23	0.979
8.0	0.0478–2.4757	–0.131 (0.022)	0.728 (0.030)	26	0.959
12.0	0.0250–2.4260	0.027 (0.013)	0.746 (0.021)	30	0.977
15.5	0.0561–5.4377	0.093 (0.010)	0.761 (0.018)	44	0.977

Note: Mean (± standard error (SE)) parameter estimates are provided for the equation $R_R = a\cdot\text{DW}^b$. Linear regressions were performed on log-transformed data. R_R is expressed in mg O_2·fish^{-1}·h^{-1}. All regressions were significant ($p < 0.0001$).

*For conversion of cod dry weight (DW) to wet weight (WW): DW = 0.217(WW) – 0.040.

size differences (e.g., Schurmann and Steffensen 1997), a value derived from the work of Saunders (1963) with adult cod. Results of the present study at four temperatures indicated that a lower value, 0.731 (eq. 8), is more appropriate for smaller (young-of-year) juveniles. The scaling of metabolism to body size can change with body size, concomitant with developmental changes (for review, see Post and Lee 1996). Allometric slopes, values for b in the equation $y = a\cdot\text{DW}^b$, often decrease from ~1.0 in young fish larvae to values closer to 0.75 in older juveniles and adults. The 3/4 power scaling law (b = 0.75) is associated with a variety of biological phenomena (West et al. 1997), and the rate of change in juvenile cod R_R with body weight does not appear to be an exception.

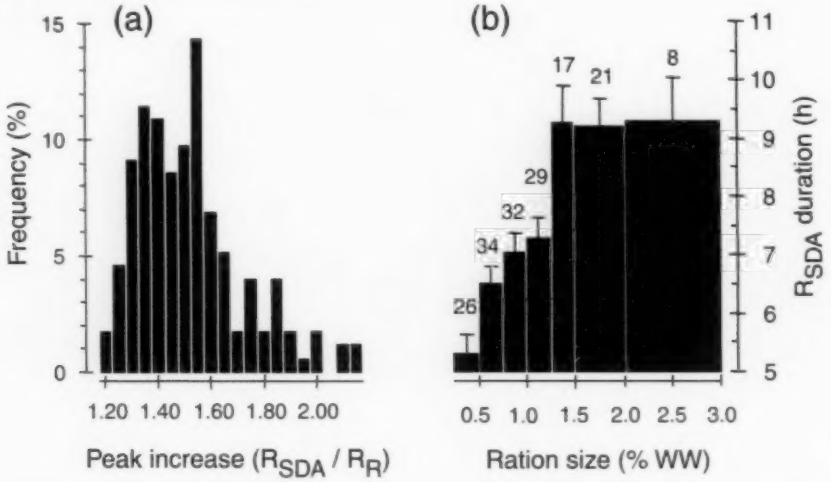
Routine energy loss and temperature

Temperature is likely the most important environmental factor affecting fish physiology. For example, most of the variability in growth (92%) among different cod stocks in the Atlantic Ocean has been explained using a model incorporating differences in mean seasonal temperature and fish age (Brander 1995). Because of the importance of temperature as a controlling factor (Fry 1957), studies evaluating temperature effects on cod respiration have been common. The Q_{10} value (eq. 2) is generally close to 2.0 for most poikilotherms, and when calculated using eq. 8 in this study, the mean Q_{10} for young-of-year juvenile cod mean R_R was 2.07. This value is similar to those for standard respiration (R_S) of larger, year-1+ juvenile cod between 5 and 15 °C and 10 and 15 °C (1.98 and 2.27, respectively; Schurmann and Steffensen (1997), weight-corrected values, their table 1) and other Q_{10} values (2.3 to 2.6) calculated for a variety of fish species (e.g., Brett and Groves 1979; Paul 1986; Keckeis et al. 2001).

The effect of temperature on bioenergetic rates is not a static variable but changes with body size and (or) develop-

© 2003 NRC Canada

Fig. 3. Attributes of feeding energy losses in juvenile Atlantic cod (*Gadus morhua*). (*a*) Frequency distribution of the peak increase in O_2 consumption rate during or shortly after feeding (R_{SDA}) relative to the prefeeding routine rate (R_R). The mean (± standard deviation) $R_{SDA\ PEAK}$ at 4.5, 8.0, 12.0, and 15.5 °C was 1.68 (0.24), 1.63 (0.23), 1.48 (0.17), and 1.51 (0.17), respectively. (*b*) The mean (± standard error) duration (h) of R_{SDA} versus consumed ration size (*n* indicated above bars). Replicates consisted of an individual chamber containing between 1 and 15 fish of similar size.



mental stage in a species. In the present study, a nonlinear interaction between body size, temperature, and routine energy loss is suggested when Q_{10} values are calculated for size-specific rates of R_R at different temperature combinations using equations in Table 2. For example, in a 0.1 g DW (3.9 cm SL) juvenile, the Q_{10} value for R_R between 4.5 and 8.0 °C (2.01) is greater than that between 12 and 15.5 °C (1.40). Similarly, in a 3.0 g DW (11.4 cm SL) juvenile, Q_{10} values are 3.23 and 1.62, respectively, for the same two temperature combinations. Temperature combinations having the lowest Q_{10} values coincide with optimal temperatures (12.0–14.3 °C) estimated for growth in similar-sized young-of-year cod (Otterlei 2000; Björnsson and Steinarsson 2002; Peck et al. 2003). Results of this study also suggest that as body size increases, so does the effect of temperature change on R_R. This is not unexpected for this species because optimum temperatures for growth in cod decrease with increasing size and age (Björnsson and Steinarsson 2002) and young small juveniles are typically encountered within a broader range of temperatures (6–20 °C) than are larger juveniles and adults (<10 °C) (Fahay et al. 1999).

Feeding energy loss

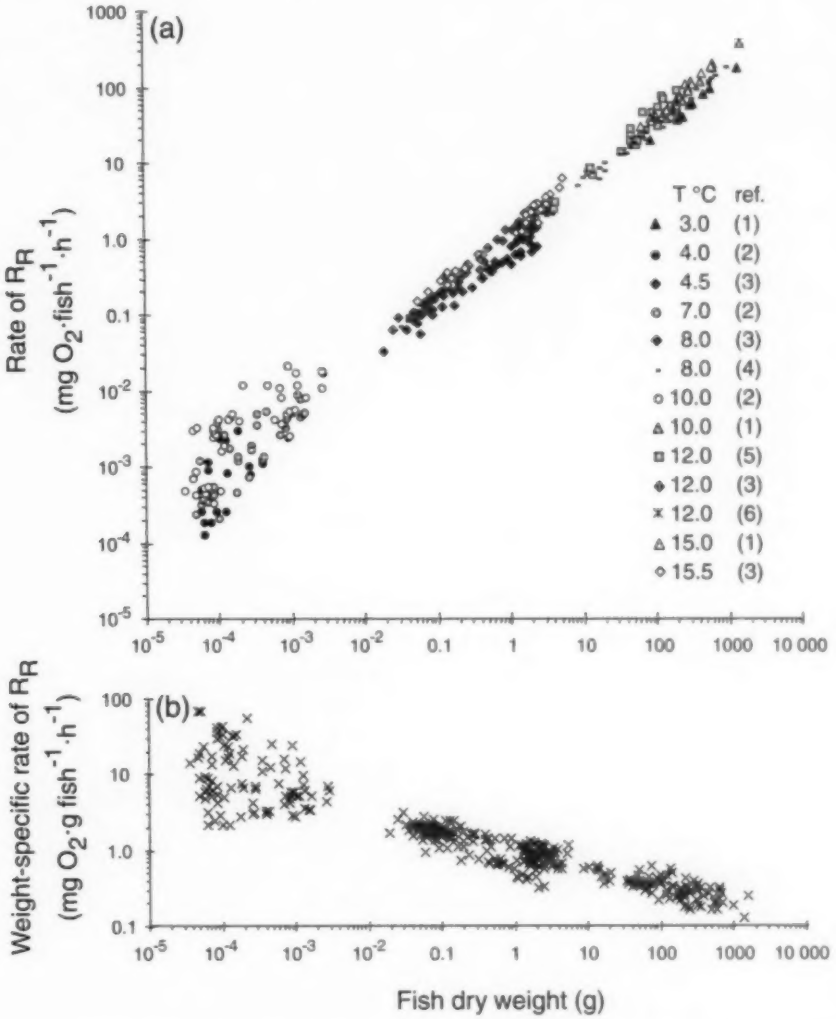
The increase of respiration rates during feeding is thought to primarily result from the costs of protein synthesis, contributing up to 44% of the increase in adult cod (Lyndon et al. 1992). Aerobic costs associated with digestion in large juvenile and adult cod may greatly limit, or sometimes exceed, the aerobic scope for activity ($R_A - R_R$) (Soofiani and Priede 1985), and increases in swimming activity have been shown to prolong the $R_{SDA\ DUR}$ (Blaikie and Kerr 1996). In adult cod, therefore, tradeoffs are thought to exist in the energy costs associated with feeding and activity. Some of the results of the present study using young juveniles contrast those found for adults. Principal differences include a shorter duration of the feeding effect at similar ration sizes and a lower proportion of food energy lost to R_{SDA}, both of which imply lower energetic costs owing to R_{SDA} in young juveniles.

In larger (~30–80 g WW) juvenile cod, $R_{SDA\ PEAK}$ was measured to be 1.32 and 1.71 times greater than prefeeding (routine) rates and increased with both feeding level and temperature from 7 to 15 °C (Soofiani and Hawkins 1982). Our results were similar with respect to the mean $R_{SDA\ PEAK}$, which was between 1.48 and 1.68 times greater than routine rates. Not surprisingly, $R_{SDA\ DUR}$ was much shorter (mean = 7.3 h) for the smaller juveniles in our study compared with that (1 to 2 days) for larger juveniles and adults (Soofiani and Hawkins 1982; Lyndon et al. 1992; Blaikie and Kerr 1996). The shorter duration is attributable to increased rates of digestion and egestion in smaller fish compared with larger fish fed similar percentage body weight rations. The lack of a substantial temperature effect on $R_{SDA\ PEAK}$ in our study may represent another mechanism whereby juveniles can exploit (Fahay et al. 1999) and grow well (Björnsson and Steinarsson 2002) at higher temperatures compared with adults.

In the present study, small, year-0 juveniles lost ~4% of the consumed food energy via $R_{SDA\ MAG}$ compared with losses of 7–17% for larger juveniles (Soofiani and Hawkins 1982). The $R_{SDA\ MAG}$ is influenced by both the type of food consumed and the size of the meal (Lyndon et al. 1992). The protein content (55%) and energy content (20.82 J·mg DW^{-1}) of the diet used in the present study were sufficiently high as to not bias our results (decreasing energy and protein content decrease the $R_{SDA\ MAG}$). Furthermore, growth efficiencies of young-of-year cod fed this diet were high, in some instances >30% (Peck et al. 2003), implying high digestibility and nutritive quality. Pre- and post-settlement juvenile cod (<12.5 cm TL) consume a variety of prey, mostly invertebrates (zooplankton), as well as fish, with the magnitude of piscivory increasing with increasing juvenile body size (Robb and

© 2003 NRC Canada

Fig. 4. (*a*) Routine respiration rate (R_R) versus dry weight (DW) for larval, juvenile, and adult Atlantic cod (*Gadus morhua*) at different temperatures: (1) Saunders 1963; (2) Laurence 1978; (3) this study; (4) M.A. Peck, unpublished data; (5) Edwards et al. 1972; (6) J.-P. Herrmann (University of Hamburg, Olbersweg 24, D-22767, Germany), unpublished data. (*b*) R_R data expressed as weight-specific rates.



Hislop 1980; Keats et al. 1987). Habitat transitions coincide with diet shifts, which affect cod activity patterns (e.g., Lough and Potter 1993) and, in other species, the level of metabolic enzymes (Sherwood et al. 2002). The influence of different prey types and habitat-related activity patterns were not evaluated in the present investigation, although shifts in diet and behavior during the juvenile settlement phase will undoubtedly affect rates of bioenergetic parameters.

Other studies

Considerable research has been conducted investigating the routine metabolism of Atlantic cod. The data presented in this study bridge the gap between respiration measurements performed on larvae (e.g., Laurence 1978; Hunt von Herbing and Boutilier 1996) and larger juveniles and adults (e.g., Saunders 1963; Edwards et al. 1972; Schurmann and Steffensen 1997). In general, good agreement was found between studies in terms of measured rates of R_R after taking into account the allometric relationship between physiological rates and body sizes in cod (Fig. 4*a*). Where possible, the data from previous investigations were combined with those of this study in a multiple linear regression:

$$(12)\quad R_R = 0.509(\pm 0.039)(\mathrm{DW})^{0.728(\pm 0.005)}\exp^{(T\cdot 0.068(\pm 0.007))},$$

$$R^2 = 0.985,\ n = 381$$

where mean (±SE) parameter estimates are provided, R_R is expressed in mg O_2·fish^{-1}·h^{-1} and DW is expressed in grams. The rate of energy loss in J·fish^{-1}·h^{-1} can be calculated by substituting a mean (±SE) value of 6.921 (0.530) for 0.509 (0.039) in eq. 12. This equation describes the effects of T

© 2003 NRC Canada

and body size (DW) on routine metabolic energy losses by Atlantic cod over the eight orders of magnitude difference in fish size from larvae to adults and should prove useful where average temperature- and size-specific values of energy loss are needed for this species.

A comparison of the various studies performed on cod also reveals that although the range in scaling of R_R with body size is similar in larvae (0.687 to 0.850; Laurence 1978), young-of-year juveniles (0.677 to 0.761; this study), and larger (older) juveniles and adults (0.820; Saunders 1963), measured rates of larval R_R are considerably more variable. This is especially apparent when log-transformed rates are expressed on a weight-specific basis (Fig. 4*b*). Variability in larval respiration rates may be an important, inherent characteristic of this life stage. However, variability in measured rates of R_R may result from a number of sources including different methodologies (e.g., protocols and equipment), as well as interstock physiological differences (e.g., Hunt von-Herbing and Boutilier 1996). Given the variability in larval metabolic rates and an expectation that larval rates may scale differently with body size and temperature than those of juveniles and adults (e.g., Post and Lee 1996), a more rigorous analysis, beyond the scope of this study, seems warranted. Such an analysis would be especially useful because larval gadid modeling efforts (e.g., Werner et al. 1996; Hinrichsen et al. 2002) rely on these data (see Buckley et al. 2000).

In conclusion, results of the present study suggest bioenergetic differences between young-of-year juveniles and larger (older) juvenile and adult cod (e.g., different allometric scaling factors, energy losses as a result of feeding, and temperature effects). Differences in the physiology of cod and other fish species with size and stage likely result from mechanisms acting to promote increased growth efficiency during early life. Growth efficiency is generally higher in smaller, younger fish and declines with increasing body size in many species (Brett and Groves 1979; Keckeis et al. 2001), including Atlantic cod (Hansson et al. 1996). The results of this study highlight the need for additional, basic physiological research on early larval and juvenile stages of marine fish species. Understanding the physiological differences between young-of-year juveniles and older, larger conspecifics should provide additional insight as to how young juveniles cope with the increased energetic burden imposed by relatively high rates of somatic growth within environments having greater risks of mortality as the result of starvation and predation.

Acknowledgements

Helpful comments on this manuscript were received from E. Caldarone, E. Durbin, and C. Oviatt. Additional respiratory data were provided by A. Temming and J.-P. Herrmann (University of Hamburg). Engineering assistance was provided by E. Requintina and H. Silverbush. We are greatly indebted to the employees and support staff of both the U.S. Environmental Protection Agency – Atlantic Ecology Division and the U.S. National Oceanic and Atmospheric Administration – National Marine Fisheries Service (NOAA/NMFS) Narragansett Laboratory for access to and use of their facilities. This study was supported by NOAA / University of Rhode Island Cooperative Marine Education and Research grant No. NA77FE0494 and University of New Hampshire Open Ocean Aquaculture Grant No. NA16RP1718.

References

Björnsson, B., and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **59**: 404–502.

Blaikie, H.B., and Kerr, S.R. 1996. Effect of activity level on apparent heat increment in Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. **53**: 2093–2099.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. **52**: 1–10.

Brett, J.R., and Groves, T.D.D. 1979. Physiological energetics. *In* Fish physiology. Vol. VIII. Bioenergetics and growth. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 279–351.

Buckley, L.J., Lough, R.G., Peck, M.A., and Werner, F.E. 2000. Larval Atlantic cod and haddock growth models, metabolism, ingestion, and temperature effects. Can. J. Fish. Aquat. Sci. **57**: 1957–1960.

Campana, S.E. 1996. Year-class strength and growth rate in young Atlantic cod, *Gadus morhua*. Mar. Ecol. Prog. Ser. **135**: 21–26.

Campana, S.E., Frank, K.T., Hurley, P.C.F., Koeller, P.A., Page, F.H., and Smith, P.C. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 171–182.

Edwards, R.R.C., Finlayson, D.M., and Steele, J.H. 1972. An experimental study of the oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. **8**: 299–309.

Fahay, M.P., Berrien, P.L., Johnson, D.L., and Morse, W.W. 1999. Essential fish habitat source document: Atlantic cod, *Gadus morhua*, life history and habitat characteristics. U.S. NOAA Tech. Memo. NMFS-NE-124.

Fry, F.E.J. 1957. The aquatic respiration of fish. *In* The physiology of fishes. Vol. I. *Edited by* M.E. Brown. Academic Press, New York. pp. 1–63.

Green, E.J., and Carritt, D.E. 1967. New tables for oxygen saturation of seawater. J. Mar. Res. **25**: 140–147.

Hansson, S., Rudstam, L.G., Kitchell, J.F., Hilden, M., Johnson, B.L., and Peppard, P.E. 1996. Predation rates by North Sea cod (*Gadus morhua*) — predictions from models on gastric evacuation and bioenergetics. ICES J. Mar. Sci. **51**: 107–114.

Hinrichsen, H.-H., Möllmann, C., Voss, R., and Kornilovs, G. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. Can. J. Fish. Aquat. Sci. **59**: 1858–1873.

Hunt von Herbing, I., and Boutilier, R.G. 1996. Activity and metabolism of larval Atlantic cod (*Gadus morhua*) from Scotian Shelf and Newfoundland source populations. Mar. Biol. **124**: 607–617.

Keckeis, H., Kamler, E., Bauer-Nemeschkal, E., and Schneeweiss, K. 2001. Survival, development and food energy partitioning of nase larvae and early juveniles at different temperatures. J. Fish Biol. **59**: 45–61.

Keats, D.W., Steele, D.H., and South, G.R. 1987. The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundalnd. Can. J. Zool. **65**: 1273–1287.

Laurence, G.C. 1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. **50**: 1–7.

© 2003 NRC Canada

Lough, R.G., and Potter, D.C. 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. U.S. Fish. Bull. **91**: 281–303.

Lyndon, A.R., Houlihan, D.F., and Hall, S.J. 1992. The effect of short-term fasting and single meal on protein synthesis and oxygen consumption in cod, *Gadus morhua*. J. Comp. Physiol. B, **162**: 209–215.

Northby, J.A. 1976. A comment on rate measurements in open systems. Limnol. Oceanogr. **21**: 180–182.

Otterlei, E. 2000. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*). Ph.D. thesis, University of Bergen, Bergen, Norway.

Paul, A.J. 1986. Respiration of juvenile pollock, *Theragra chalcogramma* (Pallas), relative to body size and temperature. J. Exp. Mar. Biol. Ecol. **97**: 287–293.

Peck, M.A., Buckley, L.J., Caldarone, E.M., and Bengtson, D.A. 2003. Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Mar. Ecol. Prog. Ser. **251**: 233–243.

Post, J.R., and Lee, J.A. 1996. Metabolic ontogeny of teleost fishes. Can. J. Fish. Aquat. Sci. **53**: 910–923.

Robb, A.P., and Hislop, J.R.G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. J. Fish Biol. **16**: 199–217

Ross, L.G., and McKinney, R.W. 1988. Respiratory cycles in *Oreochromis niloticus* (L), measured using a six-channel microcomputer-operated respirometer. Comp. Biochem. Physiol. A Comp. Physiol. **89**: 637–643.

SAS. 1989. SAS/STAT® user's guide version 6. 4th ed. Vol. 2. SAS Institute Inc., Cary, N.C.

Saunders, R.L. 1963. Respiration of the Atlantic cod. J. Fish. Res. Board Can. **20**: 373–385.

Schurmann, H., and Steffensen, J.F. 1997. Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. J. Fish Biol. **50**: 1166–1180.

Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. **59**: 229–241.

Soofiani, N.M., and Hawkins, A.D. 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua*. J. Fish Biol. **21**: 577–592.

Soofiani, N.M., and Priede, I.G. 1985. Aerobic metabolic scope and swimming performance in juvenile cod, *Gadus morhua* L. J. Fish Biol. **26**: 127–138.

Werner, F.E., Perry, R.I., Lough, R.G., and Naimie, C.E. 1996. Trophodynamics and advective influences on Georges Bank larval cod and haddock. Deep-Sea Res. Part II Top Stud. Oceanogr. **43**: 1793–1822.

West, G.B., Brown, J.H., and Enquist, B.J. 1997. A general model for the origin of allometric scaling laws in biology. Science (Wash., D.C.), **276**: 122–126.

© 2003 NRC Canada

Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation

James E. Garvey and Elizabeth A. Marschall

Abstract: For fish at high latitudes, short growing seasons should constrain size-at-age, although the converse often occurs. We used a dynamic state variable model to find energy allocation strategies to length, fat, and ovaries that maximize expected egg production of largemouth bass (*Micropterus salmoides*). We determined how latitudes and rations affect optimal allocation and then simulated growth using optimal strategies. A theoretical reciprocal transplant explored how latitude-specific optimal strategies affected growth at other latitudes. At low ration, allocation and growth were similar among latitudes, with length selected in small individuals and reproductive tissue and fat in large counterparts. At high rations, low-latitude fish invested most energy to length and reproduction; high-latitude fish allocated to length during summer and fat during fall and developed ovaries earlier in the year. Transplants revealed that smaller size-at-age occurs in the north than in the south, consistent with field patterns for largemouth bass. Although northern strategies allowed fish to be successful in the south, southern strategies were unsuccessful in the north. Latitude-specific energetic adaptations may compromise success of fish transplanted beyond their native distribution.

Résumé : Chez les poissons des hautes latitudes, les saisons de croissance courtes devraient réduire les tailles à un âge donné, alors que souvent c'est le contraire qui se produit. Un modèle à variables dynamiques nous a permis d'identifier les stratégies d'allocation de l'énergie à la croissance en longueur, à la graisse et aux ovaires qui maximisent la production attendue d'oeufs chez l'achigan à grande bouche (*Micropterus salmoides*). Nous avons déterminé comment la latitude et la ration alimentaire affectent l'allocation optimale, pour ensuite faire une simulation de la croissance dans des conditions de stratégies optimales. Un transfert réciproque simulé a servi à explorer comment les stratégies optimales spécifiques à une latitude affectent la croissance aux autres latitudes. Lorsque les rations alimentaires sont faibles, l'allocation et la croissance sont semblables à toutes les latitudes : la longueur est favorisée chez les petits individus et les tissus reproducteurs et adipeux chez les plus grands. Lorsque les rations sont fortes, les poissons des basses latitudes investissent la majorité de leur énergie dans la croissance en longueur et dans la reproduction; les poissons des latitudes élevées allouent leur énergie à la croissance en longueur en été, aux tissus adipeux en automne et au développement des ovaires tôt dans l'année. Les transferts indiquent que les tailles spécifiques aux âges sont plus faibles dans le nord que dans le sud, ce qui correspond à la situation de l'achigan à grande bouche en nature. Bien que les stratégies nordiques permettent aux poissons de se maintenir avec succès dans le sud, les stratégies du sud ne fonctionnent pas dans le nord. Les adaptations énergiques spécifiques à la latitude peuvent donc mettre en péril les transplantations de poissons au-delà de leur répartition d'origine.

[Traduit par la Rédaction]

Introduction

Bergmann's rule suggests that the body size of animals should increase with increasing latitude (Lindsey 1966). For many widely distributed poikilotherms that grow indeterminately, including fish, the applicability of this rule has been questioned (e.g., Roff 1980, 1986). These species must contend with shorter growing seasons and longer winters as latitude increases (Mousseau 1997). Warm summers foster growth, whereas cold winters may completely arrest it. As such, fish and other aquatic poikilotherms at high latitudes may have a limited opportunity for growth and, thus, may ultimately be smaller than conspecifics at low latitudes. Latitudinal differences in growth and body size should be particularly relevant during the first year of life, because increasing size often increases the probability of first-winter survival and ultimately recruitment to the population (Garvey et al. 1998).

Body size at any time is the result of interactions among energy intake, metabolic costs, and the allocation of net energy to different structures and activities. Patterns of energy allocation affect an organism's level of energy stores and degree of gonadal development. Seasonal changes in body com-

Received 23 December 2002. Accepted 31 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 9 September 2003.
J17256

J.E. Garvey.[1] Fisheries and Illinois Aquaculture Center, Department of Zoology, Southern Illinois University, Carbondale, IL 62901-6511, U.S.A.
E.A. Marschall. Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 1314 Kinnear Road, Columbus, OH 43212-1156, U.S.A.

[1]Corresponding author (e-mail: jgarvey@siu.edu).

 doi: 10.1139/F03-083 © 2003 NRC Canada

position must occur in anticipation of conditions that affect survival or reproductive success (Shul'man 1974; Weatherley and Gill 1987; Bunnell and Marschall 2003). Energy reserves should increase before predictable times of low food availability such as winter, whereas gonads should develop in advance of the reproductive season. As individuals allocate energy to gonads or fat reserves, they necessarily reduce their allocation to permanent structural growth (herein referred to as "body size"). Because the maximum fat reserves and gonadal mass that an individual can hold generally increase with body size, by allocating energy to fat or gonads rather than body size, an individual may actually be compromising its future reproductive output potential. An appropriate balance of these options should be quite important at high latitudes as reduced temperature limits energetic intake.

Although it may be clear that seasonal changes in body composition incur fitness consequences, the issue of how body composition precisely relates to fitness is complex. For example, because of allometric morphological relationships, increased growth in length often increases fat reserve capacity while reducing mass-specific metabolic rate in fish. When energy intake is limited, energy stores are depleted less rapidly with increasing size. Conversely, accumulating energetically dense fat tissue requires a considerable energetic investment that must be met at the cost of reduced growth in length. The importance of energy stores and metabolic rate should change with latitude, as mean temperature and duration of winter change. How allocation strategies vary along environmental gradients should greatly affect growth, reproductive success, and thereby the geographic distribution of species. Indeed, seasonal patterns in body composition often vary among populations within a species and can be genetically determined (Mousseau and Roff 1989).

Given the role that energy allocation patterns may play in determining size across a latitudinal gradient, particularly during the first year of life, understanding the trade-offs that drive energy allocation will contribute to the discussion of whether and why aquatic poikilotherms should follow Bergmann's rule or its converse. Reasoning in support of a converse to Bergmann's rule for poikilotherms generally is based on the simple direct interaction between temperature and physiology: consumption and metabolic rates decline with decreasing temperature, resulting in small body size at high latitudes. Reasoning in support of Bergmann's rule generally is based on the strength of selection for large size in cold environments: either the relative advantage of large size is high or the relative disadvantages of getting to a large size are low (Partridge and Coyne 1997).

Dynamic state variable models (Mangel and Clark 1988) are perfectly suited to consider state- and condition-dependent limitations in the context of finding evolutionarily optimal responses, which maximize expected lifetime fitness. We developed dynamic-state variable models to find differences in optimal energy allocation between northern and southern latitudes of a fish with temperature-dependent consumption and growth potential. This discrete-time optimization method uses backward iteration to find strategies that maximize expected future lifetime fitness in problems involving a sequence of decisions (Bellman 1957; Mangel and Clark 1988). We have embedded a bioenergetic algorithm within this dynamic model that calculates consumption and metabolic rates as functions of temperature and body mass (Wright et al. 1999).

Our ultimate goal was to weigh how latitudinal differences in temperature and related factors affect seasonal changes in body composition, body size, and reproductive output of widely distributed fish and other aquatic poikilotherms. We first explored optimal energy allocation patterns across a latitudinal gradient. Next, we simulated the growth that arises from these optimal patterns to compare size-at-age and reproductive potential between latitudes. And finally, we performed a theoretical reciprocal-transplant experiment by simulating the optimal high-latitude allocation patterns in low-latitude conditions and optimal low-latitude allocation patterns in high-latitude conditions. These results provide insight into patterns of growth of widely distributed species and options for their conservation at geographic scales not typically addressed by managers.

Methods

Study species

Largemouth bass (*Micropterus salmoides*) is a widely distributed fish species found in freshwater lakes and rivers from 25 to 47°N latitude in North America. As such, separate populations of this species experience very different seasonal temperatures. At any latitude, this species' distribution is cosmopolitan, including aquatic ecosystems of a variety of levels of productivity, types of prey assemblages, and combinations of physical characteristics (e.g., temperature stratification). The bioenergetics of this species are generally well understood, and underlying relationships have been incorporated into a mass-balance model that has produced robust, field-verified results (Rice and Cochran 1984). Because this model and empirical evidence demonstrate that temperature strongly influences growth in largemouth bass as well as other fishes, seasonal variation in temperature should drive much of the variation in energy allocation patterns and reproductive success throughout this species' range.

Dynamic state variable model

For each week t ($t = 0, 1,..., 51$, where $t = 51$ is the week of spawning) of each year y ($y = 0, 1,..., 5$) in the dynamic state variable model, we calculated the maximum expected future lifetime fitness, $F(L, w, r, t, y)$, of a female largemouth bass of body length L (total length, mm), having fat reserves at w proportion of their maximum and having reproductive tissue at r proportion of its maximum. Maximum fat reserves and reproductive tissue are assumed to be increasing functions of L. Some fat reserves are necessary for survival; thus largemouth bass with $w = 0$ die.

For any given week, a modeled fish compares expected future fitness from each possible allocation strategy $\boldsymbol{\phi}(\boldsymbol{\phi} = (\phi_L, \phi_w))$ in which the fish allocates a proportion ϕ_L of that week's net energy intake to growth in length, a proportion ϕ_w to growth in fat reserves, and a proportion $1 - \phi_L - \phi_w$ to growth in reproductive tissue. On week 51, the fish spawns, receiving a fitness payoff that is a function of the state of its

© 2003 NRC Canada

reproductive tissue. Simulations ended after 6 years, allowing fish potentially to spawn six times.

An allocation strategy ϕ during a given week t (t = 0, 1,..., 50) by a fish having state values L, w, and r results in state values the following week of $L'(\phi)$, $w'(\phi)$, and $r'(\phi)$, respectively. The fish chooses the allocation strategy that maximizes expected lifetime fitness beginning at the present, such that during nonspawning weeks

$$(1) \quad F(L,w,r,t,y) = \max_{\phi} F(L'(\phi), w'(\phi), r'(\phi), t+1, y)$$

During week t = 51, an allocation strategy ϕ results in new state values at the beginning of the next year (which begins the week after spawning) of $L''(\phi)$, $w''(\phi)$, and $r''(\phi)$ such that

$$(2) \quad F(L,w,r,51,y) = Q(L,w,r) + \max_{\phi} F(L''(\phi), w''(\phi), r''(\phi), 0, y+1)$$

where $Q(L,r)$ is the reproductive output (number of eggs) from spawning at the end of year y.

The actual amount of energy allocated to each function is limited by the amount of food ingested in a given week. We represent energy ingested as a proportion ρ of the maximum possible (C_{max}; calories·week^{-1}) for a largemouth bass of that size:

$$(3) \quad C_{max} = 0.33M^{0.675}z \times 7 \times 1000$$

where M is wet mass (g) excluding fat and is calculated as $M = (1.35 \times 10^{-5})L^{2.98}$ (Trebitz 1991) and z is a temperature-dependent multiplier (see Rice et al. 1983). The function for C_{max} derives from data in Niimi and Beamish (1974) that was modeled by Rice et al. (1983). We assumed a prey caloric density of 1000 calories·g^{-1} (Wright et al. 1999). Fat could make up no more than 3% of total wet mass (Miranda and Hubbard 1994; Oster 2002), and reproductive tissue could make up no more than 10% of total wet mass (Carlander 1977). We used W to represent grams of body mass in fat ($W = w(0.03M)$) and R to represent grams of reproductive tissue $R = r(0.1M)$). Weekly metabolic costs α (calories·week^{-1}) were estimated as a function of temperature τ (°C) and total wet mass N (g), including mass of the current fat and reproductive tissue, $N = M + W + R$. These variables were included in a metabolic cost function described by Trebitz (1991):

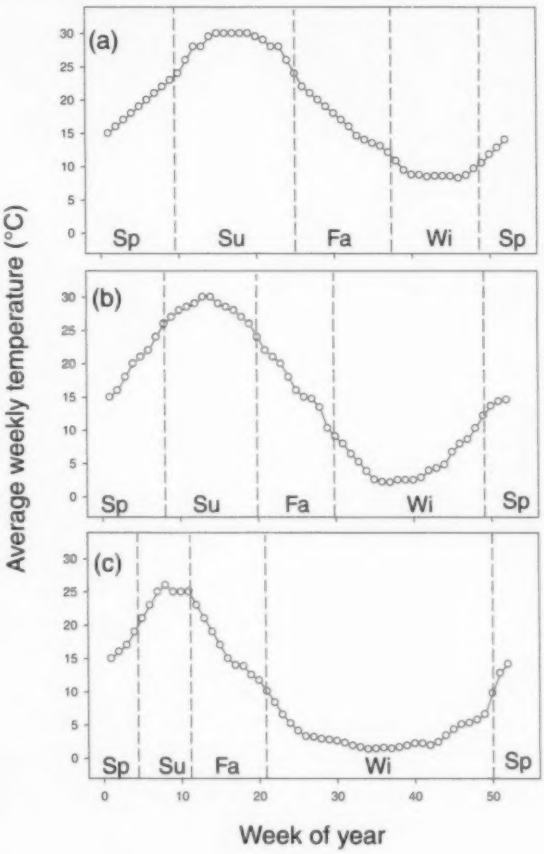
$$(4) \quad \alpha = 0.0868N^{-0.355}e^{0.0811\tau+0.0196}K_{act}0.078 \times 7 \times 1000$$

where we assume that largemouth bass caloric density is 1000 calories·g^{-1} (Garvey et al. 1998) and K_{act} is an activity multiplier that causes small largemouth bass (<60 mm) to grow at realistic rates (Trebitz 1991):

$$(5) \quad K_{act} = \begin{cases} 1 & \text{for } \tau < 10\ ^\circ\text{C} \\ 1.1N^{-0.1} & \text{for } \tau \geq 10\ ^\circ\text{C and } N \leq 2.594\ \text{g} \\ 1.0198 & \text{for } \tau \geq 10\ ^\circ\text{C and } N > 2.594\ \text{g} \end{cases}$$

Weekly costs I (calories·week^{-1}) due to egestion and excretion were estimated as a function of temperature, total mass, and ration according to the model by Trebitz (1991):

Fig. 1. Weekly average temperatures from (*a*) south- (33°N; Ludsin and DeVries 1997), (*b*) middle- (40°N; Garvey et al. 1998), and (*c*) north- (46°N; North Temperate Lake, Long Term Ecological Research (LTER) program, 1992–1994) latitude aquatic systems. Spring (Sp), summer (Su), fall (Fa), and winter (Wi) periods are delineated by vertical broken lines. Largemouth bass (*Micropterus salmoides*) at each latitude spawned at week 51, when temperature reached 15 °C.



$$(6) \quad I = [\text{SDA}(\tau,N,\rho C_{max}) + B(\tau,N,\rho C_{max}) + S(\tau,N,\rho C_{max})] \times 7 \times 1000$$

where SDA is specific dynamic action (calories), B is feces (calories), and S is excretion (calories). Again, we assumed caloric density of prey was 1000 calories·g^{-1} and summed costs for each week. Costs of converting consumed energy into each type of body mass were assumed to be included in I. Weekly temperatures (τ) were weekly means measured in natural systems at southern (33°N; Alabama ponds), middle (40°N; Ohio reservoirs), and northern (46°N; Wisconsin lakes) latitudes (Fig. 1; Wright et al. 1999).

State dynamics

We assumed that metabolic costs are paid from energy ingested each week. Costs in excess of energy consumed are paid from fat reserves. Thus, length, proportion of maximum

© 2003 NRC Canada

fat reserves, and proportion of maximum reproductive tissue change with each nonspawning time step as a function of net energy intake (which is a function of gross energy intake, temperature, and body size) and energy allocation according to the following equations:

$$(7)\quad L'(\boldsymbol{\phi}) = \begin{cases} L + (4.22(\phi_L(\rho C_{\max} - \alpha - I))^{0.3357}) & \text{for } \rho C_{\max} > \alpha + I \\ L & \text{for } \rho C_{\max} \le \alpha + I \end{cases}$$

where the coefficient (4.22) and exponent (0.3357) derive from a conversion from total calories to total length (Garvey et al. 1998),

$$(8)\quad w'(\boldsymbol{\phi}) = \begin{cases} \dfrac{W + \phi_w(\rho C_{\max} - \alpha - I)}{0.03M'} & \text{for } \rho C_{\max} > \alpha + I \\ \dfrac{W + (\rho C_{\max} - \alpha - I)}{0.03M'} & \text{for } \rho C_{\max} \le \alpha + I \end{cases}$$

where M' is the somatic wet mass, excluding gonads, of a fish of length $L'(\boldsymbol{\phi})$ and

$$(9)\quad r'(\boldsymbol{\phi}) = \begin{cases} \dfrac{R + (1 - \phi_L - \phi_w)(\rho C_{\max} - \alpha - I)}{0.1M'} & \text{for } \rho C_{\max} > \alpha + I \\ \dfrac{R}{0.1M'} & \text{for } \rho C_{\max} \le \alpha + I \end{cases}$$

Length is truncated to a maximum of 485 mm, because growth of largemouth bass is asymptotic. When new state values were intermediate between discrete values used in the model, we calculated expected fitness using trilinear interpolation (Press et al. 1992).

Reproduction

We assumed that fish can spawn if they are at least 250 mm long and $r = 1$. During weeks when spawning occurs (i.e., when $t = 51$), a spawning fish uses all of its reproductive mass such that $r''(\boldsymbol{\phi}) = 0$. Fitness is expressed as the number of eggs spawned.

$$(10)\quad Q(L, r) = \begin{cases} g(L) & \text{for } L \ge 250 \text{ mm and } r = 1 \\ 0 & \text{otherwise} \end{cases}$$

where $g(L)$ is the number of eggs spawned, a function of female body size ($g(L) = 5.633L^{1.433}$; Carlander 1977).

Experimental design

Energy allocation strategies should underlie differences in growth across a latitudinal gradient. To predict how growth differs across latitudes, we used the dynamic state variable model to ask how temperature regimes associated with different latitudes (Alabama, Ohio, and Wisconsin; Fig. 1) affected optimal resource allocation patterns. We combined this with three constant-ration treatments in which fish consumed either $\rho = 0.3$, 0.6, or 0.9 of their $C_{\max}$ for the entire year, except when temperatures fell below 6 °C and feeding ceased ($\rho = 0$) (Garvey et al. 1998). For each latitude × food availability treatment, we calculated the optimal allocation strategy for each combination of state values: $w = 0.2, 0.4, \ldots, 1.0$; $r = 0, 0.2, \ldots, 1.0$; and $L = 50$ to 485 by 15-mm increments. For graphical analysis, allocation results were averaged within temperature-dependent "seasons" for each modeling treatment. Seasons at each latitude were divided into winter (<10 °C), spring (>10 °C and <25 °C, following winter), summer (>25 °C), and fall (>10 and <25 °C, following summer; Fig. 1). Because this modeling exercise generated a large data array (greater than 2.9 million elements), we selected subsets of expected fitness and seasonal energy allocation results that spanned the range of state values and latitudes.

To determine how optimal allocation decisions affected patterns of growth and body size, we used the full array of decisions generated by the dynamic state variable model to simulate weekly growth of an age-0 largemouth bass with $L = 50$ mm, $w = 0.2$, and $r = 0$ starting at $t = 0$ and $y = 0$ and continuing through $t = 51$ and $y = 5$. Growth was simulated using the same bioenergetic routines and combinations of rations and seasonal temperatures used in the dynamic state variable experimental design. Largemouth bass greater than 250 mm total length and $r = 1.0$ spawned at $t = 51$ of each year, resulting in $r = 0$ the following week. Proportional allocation decisions for length, fat, and reproductive states intermediate between values generated by the dynamic state variable model were estimated with trilinear interpolation.

Theoretical reciprocal transplants

Simulation results showed that fish grew in length more quickly at low latitudes than at high latitudes (see Results). To assess what portion of this growth difference was due to the direct effect of temperature on poikilotherm growth rates and what portion was due to optimal energy allocation responses to particular temperature patterns, we performed a set of theoretical reciprocal transplants. By "transplanting" fish with allocation responses that are optimal in the south to an "environment" (i.e., a simulation) with temperatures representative of the north and transplanting optimal northern fish to the south, we could begin to distinguish between direct effects of temperature and potential effects of evolved energy allocation responses. Using these theoretical reciprocal transplants, we simulated growth and reproductive potential of transplanted and "native" largemouth bass to help understand the factors driving latitudinal allocation and growth differences (see Munch and Conover (2002) for similar approach).

Results

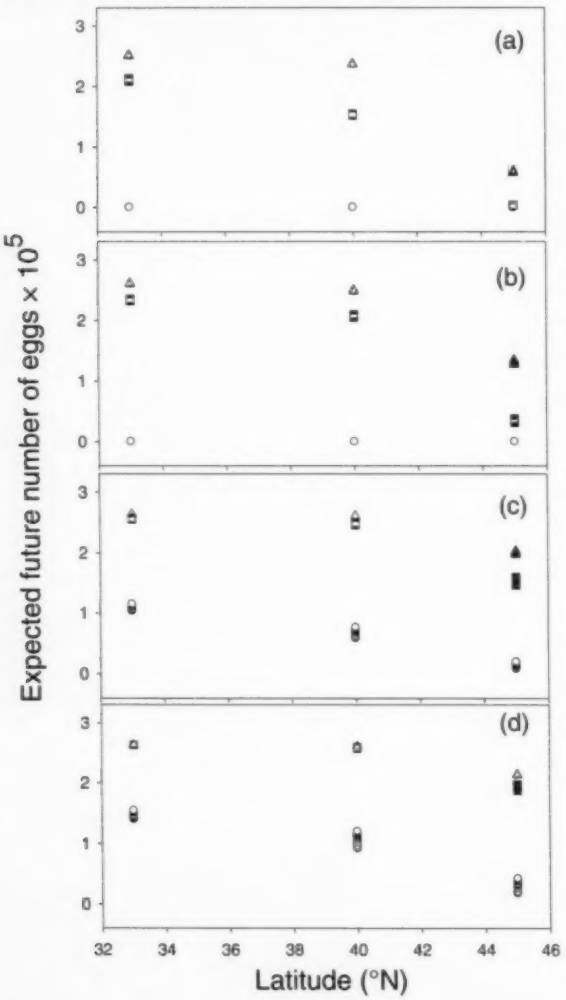
Optimal allocation patterns

Expected future fitness generally declined with increasing latitude and increased with increasing ration (Fig. 2). At low and middle rations, expected future fitness increased with body size (Fig. 2).

Optimal energy allocation to length varied as a function of ration, length, fat, and latitude. At a low ration at all latitudes, optimal proportion of energy allocated to length de-

© 2003 NRC Canada

Fig. 2. Expected number of eggs produced by a female largemouth bass (*Micropterus salmoides*) over 6 years as a function of latitude, total length at year 0, and weekly ration (i.e., proportion of maximum consumption, C_{max}) from week 0 – year 0 of the dynamic state variable model. Lengths are a subset of those modeled: (*a*) 50 mm, (*b*) 125 mm, (*c*) 275 mm, and (*d*) 350 mm. Rations are 30% (circle), 60% (square), and 90% (triangle) maximum consumption. At each latitude, length, and ration combination, the variation shown is due to the effects of varying fat reserves (20, 60, 100% of maximum) and reproductive tissue (0, 20, 60, 100% of maximum) in the model.



clined with increasing length, regardless of fat reserves (Fig. 3*a*). At an intermediate ration, a similar pattern emerged for the southern latitude (Fig. 3*b*, top panel). However, proportionally more energy was allocated to length with higher fat reserves at higher latitudes (Fig. 3*b*, middle and bottom panels). At the highest ration, fish of all lengths invested considerable energy to length in the south, regardless of fat reserves, whereas a similar pattern only occurred at higher latitudes for fish with the highest fat reserves (Fig. 3*c*).

Allocation to fat and reproduction also depended on ration, internal state, and latitude. At the lowest ration, the proportion energy allocated to fat generally increased with length at all latitudes when fat reserves were less than 100% (Fig. 3*d*). At higher rations, fat was no longer allocated at any fat reserve level at the southern latitude, whereas the same pattern that occurred at the lowest ration held for higher latitudes and rations (Figs. 3*e*, 3*f*). A similar general pattern occurred for reproductive tissue. The proportion of energy allocated to reproduction generally increased with length and fat reserves at the lowest ration at all latitudes (Fig. 3*g*). Although this pattern held for higher rations at the higher latitudes, allocation to gonads was unrelated to fat at the southern latitude at high consumption (Figs. 3*h*, 3*i*).

Simulated growth under optimal allocation

Length generally increased through time, although the rate of length increase depended on latitude and ration. At 30% maximum consumption, growth in length was poor at all latitudes, never reaching the critical length for reproduction during 6 years (Fig. 4*a*). At higher rations, growth in length was higher but declined with increasing latitude (Figs. 4*b*,4*c*).

As expected, fat abundance typically cycled annually, although the oscillations depended on latitude and ration. For fat at low rations, reserves at the southern and middle latitudes increased before summer, declined during summer, peaked again before winter, and then declined through the winter (Fig. 4*d*). Fat reserves of northern largemouth bass at low ration increased during fall and then declined during winter of each year, with no increase before summer (Fig. 4*d*). Patterns of growth in fat differed at higher rations. Although fat reserves did not cycle seasonally in the south, fat reserves increased in fall and declined in winter at the higher latitudes, with greater seasonal amplitude in the northern latitudes than in middle latitudes (Figs. 4*e*, 4*f*).

At the lowest ration, growth in reproductive tissue only occurred very late in simulations (Fig. 4*g*). At higher rations at all latitudes, reproductive tissue of sexually mature fish generally increased in fall and, by design of the model, fell to zero after spawning on week 51 (Figs. 4*h*, 4*i*). At the highest ration, fish only partially developed reproductive tissue in fall and then completed ovarian development (i.e., r = 1.0) immediately before spawning in spring (Fig. 4*i*).

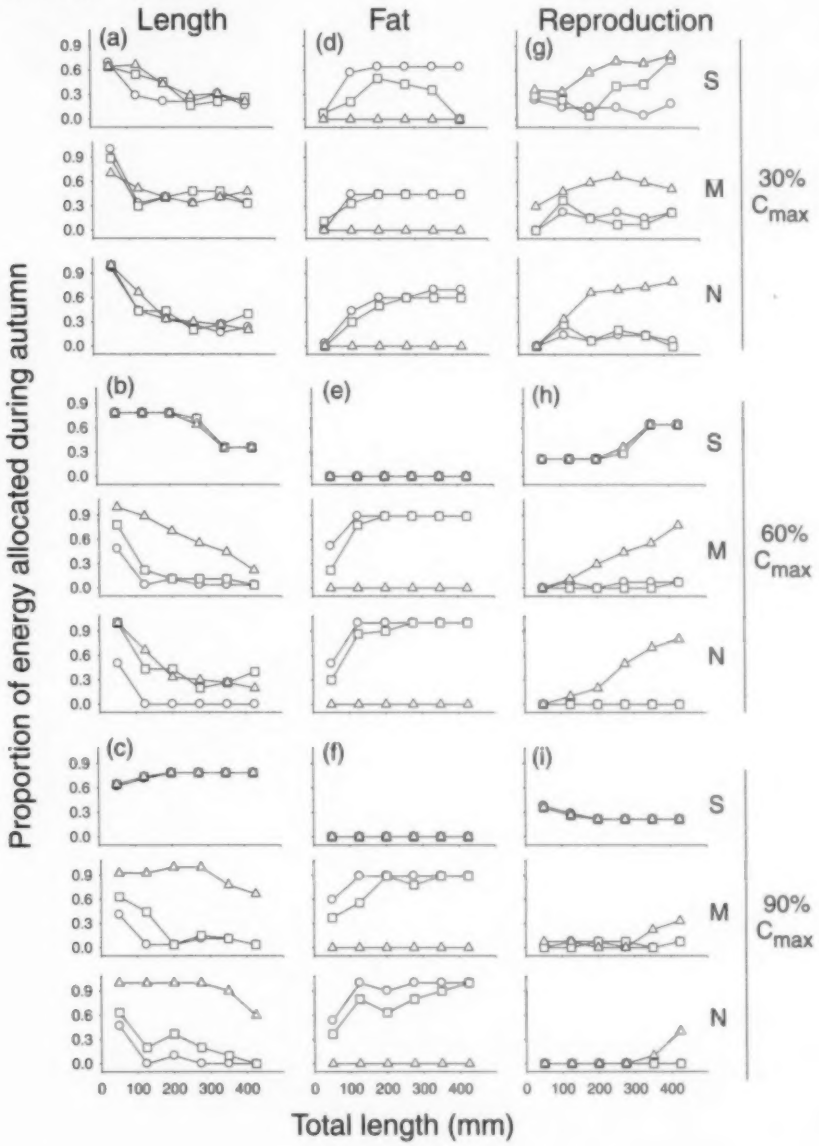
Theoretical reciprocal transplants

Largemouth bass grew in length faster in the south than in the north, regardless of whether their energy allocation pattern was optimal in the south or the north (Fig. 5*a*). Southern bass (i.e., those with optimal allocation responses in the south) grew faster than northern bass in both temperature environments (Fig. 5*a*). Although the difference was minor at northern temperatures, at southern temperatures, southern bass were about 20% longer than northern bass by age 1 (Fig. 5*a*).

Expected lifetime egg production was greater in the south than in the north, regardless of origin of the bass (Fig. 5*b*). This latitudinal fitness difference was much smaller for bass from the north than from the south. In the south, energy allocation response made little difference in expected fitness. In northern temperatures, allocation response made a large difference in expected fitness; bass with optimal northern allo-

© 2003 NRC Canada

Fig. 3. Average proportion of energy allocated to length, fat, and reproductive tissue during fall weeks as a function of fat reserves, length, and latitude in year 0 of the dynamic state variable model. Results for other seasons and subsets of data are not shown. Largemouth bass (*Micropterus salmoides*) received 30, 60, or 90% of maximum consumption (C_{max}). Reproductive tissue was at 20% of maximum. The subset of fat reserve states shown are 20% (circle), 60% (square), and 100% (triangle) of maximum capacity. Latitudes are south (S), middle (M), and north (N).



cation responses did much better than those with allocation responses optimal for southern temperatures (Fig. 5*b*).

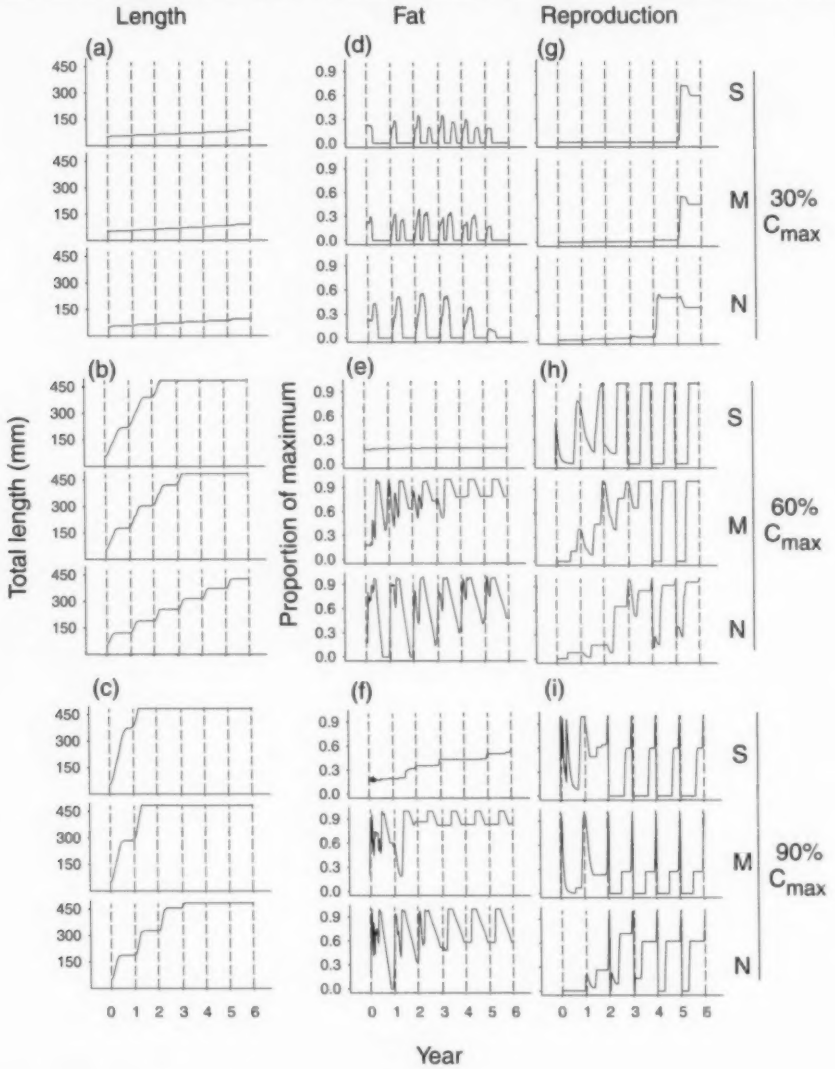
Annual timing of development of ovaries differed between the north and south and between northern and southern bass (Fig. 6). Northern bass in the north began building ovaries earlier in the year than southern bass in the south (Figs. 6*a*, 6*d*). When northern bass were transplanted to the south, they developed maximum ovary size many months before spawning (Fig. 6*b*). When southern bass were transplanted to the north, they waited too long within a year to allocate energy to reproduction and never developed enough ovary mass to reproduce (Fig. 6*c*).

Discussion

The dynamic state variable model results revealed that latitude, body size, and ration shaped patterns of optimal energy allocation in largemouth bass. Subsequent growth patterns

© 2003 NRC Canada

Fig. 4. Growth simulation results using optimal energy allocation decisions from the dynamic state variable model. Simulated largemouth bass (*Micropterus salmoides*) had initial states of 50 mm, 20% fat reserves, and 0% reproductive tissue and received either 30, 60, or 90% of maximum consumption under southern (S), middle (M), or northern (N) seasonal temperatures, respectively.



differed across latitudes as a function of these underlying energy allocation decisions. Below, we first explore the underlying allocation and growth patterns and then address their implications for variation in size along latitudinal gradients (i.e., the validity of Bergmann's rule to fish).

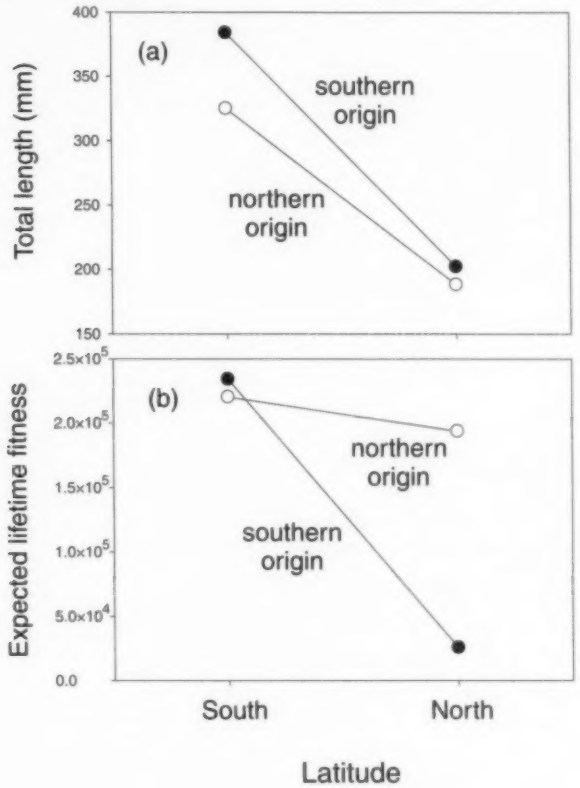
Allocation patterns and growth

Allocation of energy to fat depended on ration, fat reserves, and body size. When ration was restricted to 30% of maximum, allocation patterns were similar at all latitudes, indicating that selection in low productivity systems should generate similar growth regardless of differences in seasonal temperature. When fat reserves were low at this low ration, the smallest fish allocated to length, whereas large individuals allocated to fat until reserves were filled. For small fish, increasing length should proffer energetic benefits by reducing mass-specific metabolic costs and increasing fat storage capacity, thereby increasing survival during winter when costs exceed intake (Post and Evans 1989; Post and Parkinson 2001). In contrast, larger counterparts should have sufficient fat capacity to store fat and offset winter starvation. When fat reserves were at maximum capacity in the model, energy was still invested in length for small fish but in reproductive tissue for large fish. For large fish with relatively low mass-specific metabolic costs and abundant fat, increasing reproductive tissue to ensure spawning following winter was a priority because starvation risk was relatively low.

At higher rations, allocation strategies diverged between the southern and higher latitudes. In the south, allocation to fat reserves was no longer a priority at any size because con-

© 2003 NRC Canada

Fig. 5. (*a*) Length at age 1 and (*b*) expected lifetime fitness (number of eggs) arising from theoretical reciprocal transplants as a function of latitude. Origin of modeled largemouth bass (*Micropterus salmoides*) is either south (solid circle) or north (open circle) and growth environment is representative of either northern or southern temperatures, as indicated on the graphs. Simulated largemouth bass had initial states of 50 mm, 20% fat reserves, and 0% reproductive tissue and received 90% of maximum consumption.



sumption always exceeded metabolic needs. More energy was diverted to growth in length in small individuals and reproductive tissue in large counterparts, ensuring high growth rates, large sizes, and high future reproductive output. At higher latitudes, increased ration exerted little change on energy allocation patterns relative to patterns at low ration. Anticipation of winter metabolic costs posed similar constraints on growth, regardless of increased caloric intake during warm months. In total, these predicted results are congruent with the prediction by Shul'man (1974) that seasonal changes in energy reserves of fish should increase with increasing seasonal differences in temperature and photoperiod. Indeed, northern populations of another widely distributed species, Atlantic silversides (*Menidia menidia*), fatten in fall, but southern ones do not (Schultz and Conover 1997). In addition, age-0 largemouth bass originating from Alabama, Ohio, and Wisconsin populations reared under identical experimental conditions in Ohio during summer 1994 had fall whole-body energy densities that were consistent with the patterns in our model predictions: Wisconsin and Ohio individuals had 13% higher energy densities than Alabama counterparts (see table 1 of Fullerton et al. 2000).

Adaptive significance

There is always the risk with optimality models that although the model returns optimal strategies, the optimal strategies may produce fitness consequences that are not very different from other strategies. From the theoretical reciprocal transplants, we saw that southern conditions did not drive a strong relationship between allocation response and expected fitness. Individuals in the south could survive and reproduce regardless of whether their allocation responses were adapted to the south or the north, suggesting that optimal strategies may not be important for maintaining high fitness at this latitude. In contrast, conditions in the north were harsh enough that only individuals with allocation responses adapted to that particular environment were able to survive and reproduce there. Thus, we should expect stronger selection for optimal energy allocation responses in the north than in the south.

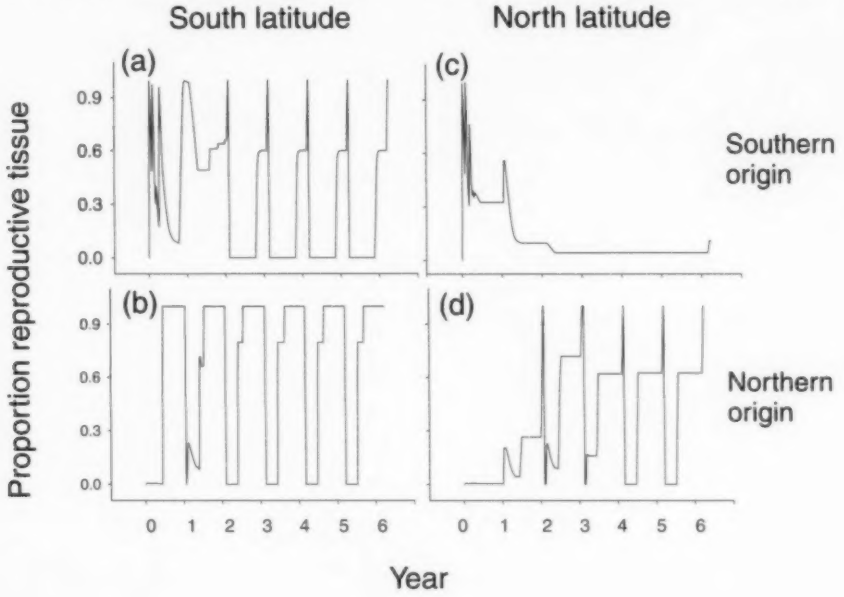
For all life stages, latitudinal adjustments in energy allocation responses ensured high expected future reproductive output up to some threshold latitude (i.e., the middle latitude). Beyond this latitude, expected fitness of small individuals declined more than large counterparts, even at high rations. Thus, the model supports the contention that insufficient fat reserves during winter and reduced growth with a short growing season may limit early survival and thus the northern extent of largemouth bass and other species, despite energetic adjustments (Garvey et al. 1998; Schultz et al. 1998). Northern latitude temperatures used in our model derive from a lake near the northern limit of largemouth bass (MacCrimmon and Robbins 1975), suggesting that the model captured the primary conditions that affect expected reproduction through negative effects on small, young fish. Similarly, a bioenergetics model predicted that low temperatures limit the northern extent of smallmouth bass (*M. dolomieu*) (Shuter et al. 1980; Shuter and Post 1990), primarily by limiting growth and survival of offspring.

Latitudinal patterns in body size

In our model, fish grew more rapidly in length at low latitudes than at high latitudes and, thus, were larger in the south than the north at any age before they reached maximum size. This is in agreement with the converse to Bergmann's rule, which has been observed in other poikilotherms (Masaki 1978; Mousseau and Roff 1989), but is in conflict with what apparently is the more common pattern of an increase in size with increasing latitude in poikilotherms, including protists, plants, and animals (see review by Atkinson (1994); Arnett and Gotelli 1999). In our model, latitudinal differences in size-at-age arose both as a simple consequence of temperature dependence of consumption and metabolic rates and as an optimal allocation response to expected temperature patterns. Both pathways produced larger fish at southern latitudes than at northern latitudes, thus supporting the converse to Bergmann's rule. A field pattern for first-year growth in largemouth bass also generally confirms this pattern in that individuals in southern populations reach larger sizes by their first fall than those in northern ones (Garvey et al. 2003).

© 2003 NRC Canada

Fig. 6. Proportion of maximum reproductive mass (ovaries) in simulated largemouth bass (*Micropterus salmoides*) from theoretical reciprocal transplants using optimal energy allocation decisions from either northern- or southern-origin largemouth bass. The growth environment was representative of either northern or southern temperatures, as indicated on the graphs. Simulated largemouth bass had initial states of 50 mm, 20% fat reserves, and 0% reproductive tissue and received 90% of maximum consumption.



Other adaptations

In addition to modifying patterns of energy allocation, other adaptations may enhance expected fitness as the length of the growing season declines and the duration of winter increases with latitude. Our model predicted that small (<125 mm) largemouth bass at northern latitudes receiving moderate rations should have a low total reproductive output over the next 6 years. Because largemouth bass often do not reach sizes >125 mm by the end of their first year in these systems (Garvey et al. 2003), other adaptive mechanisms must be in place to ensure persistence. One apparent adjustment would be to increase life span and reproductive frequency and thereby enhance lifetime reproductive output (Leggett and Carscadden 1978). Strong selection for rapid early growth rates through pathways not explored in the current model (e.g., increased foraging activity, increased assimilation efficiency) also may occur (Nicieza et al. 1994; Jonassen et al. 2000). Indeed, many widely distributed species at high latitudes have genotypes that allow them to grow more rapidly during the first year of life to counteract the shortened growing season (i.e., countergradient variation; Conover and Schultz 1995). For example, young *Menidia* (Lankford et al. 2001), striped bass (*Morone saxatilis*; Conover et al. 1997), and many other species (Conover 1990) have faster early growth rates in the north than the south, in contrast to our results.

Although not explicitly explored by our model, fish at high latitudes may reduce levels of activity and metabolic rates in the winter to reduce energetic demands for limited fat reserves during winter. Comparing predictions from mass-balance bioenergetics models for age-0 largemouth bass with growth results from overwinter pool experiments demonstrated that conventional allometric relationships used in these models overestimate energetic costs (Wright et al. 1999). Another experiment comparing winter growth across three simulated winters (i.e., low, middle, and high latitudes) revealed that small largemouth bass expend proportionately less energy during winter fasting under high-latitude seasonal temperatures than low-latitude winter conditions (Fullerton et al. 2000). Seasonal variation in body composition predicted by our model combined with additional adaptations likely allow largemouth bass to persist at latitudes higher than those predicted by simple relationships between temperature and somatic growth.

Other unexplored adaptations may exist. Although the model predicted that fish at southern latitudes typically invest energy into growth in length and not fat reserves, predator-induced foraging risk may vary inversely with latitude, with inherently riskier foraging occurring in the south (Garvey et al. 2003; also see Lankford et al. 2001). If this is true, then southern individuals may store fat reserves, reduce foraging, and ultimately reduce the rate of somatic growth when foraging is particularly risky. This scenario may be further complicated if predation risk is size-dependent in that individuals increase their survival probability by growing in length (Christensen 1996). Resolving trade-offs among risky foraging, inactivity, and energy allocation may depend on interactions among size-dependent predation, refuge, temperature, and food availability, which were not included in our model. Another option not explored in the model was flexible allocation of eggs to ovaries. Variation in fecundity at a given length may increase adaptive options for large-

© 2003 NRC Canada

mouth bass, influencing patterns of growth and expected lifetime fitness.

Implications

By exploring how seasonal variation in temperature interacts with the bioenergetics of fish, we discovered that increasing latitude should reduce the reproductive potential of aquatic poikilotherms. Although this finding is not particularly novel in itself, the nonlinear decline in expected fitness for largemouth bass suggests a dramatic reduction in population viability with a slight increase in latitude beyond some threshold. The two relatively distinct energy allocation strategies that arose suggest that two general options exist. In anticipation of low ration and high metabolic demands, an animal should store fat and begin building ovaries early in the reproductive year. If large energetic deficits are improbable, as they may be at low latitudes and high productivities, then they should increase length when small and wait longer within a reproductive year to begin building ovaries. When modeled largemouth bass with allocation responses that were optimal in the south were transplanted to the north, they actually grew in length more rapidly than did northern-adapted bass in their native environment. But these southern fish grew in length at the expense of not adding fat and not beginning early allocation to ovaries and were thus ultimately unsuccessful in the north. Early allocation to ovaries within a year is commonly observed in organisms facing low productivity later in the year immediately before spawning season (Bunnell and Marschall 2003).

Our model was built with seasonal temperature patterns that remained constant from year to year. We expect that optimal allocation strategies may also respond to predictability of these patterns (Roff 1992; Winemiller and Rose 1992). Middle latitudes may be less predictable in their seasonal temperatures than northern or southern latitudes. Bunnell and Marschall (2003) have shown that even a low chance of an unproductive spring makes optimal timing of allocation to reproduction similar to that in conditions in which spring is always harsh. Thus, we may expect some middle-latitude allocation patterns to be more similar to northern ones if environmental predictability is important.

Stocking fish is a common practice in fisheries management, with several goals including enhancing naturally reproducing populations, increasing sportfish diversity, and controlling nuisance prey species (Heidinger 1999). Although this practice is justifiable under certain circumstances (Conover 1998), our modeling results and much experimental work clearly demonstrate that fish within populations often accumulate adaptations that increase their local fitness but may prove maladaptive in new situations (also see Munch and Conover 2002). For example, we have shown that allocation responses that are optimal in the south may be unsuccessful in the north. Understanding whether these adaptations are important at extremely local scales (e.g., within individual lakes) or larger ones (e.g., within- or among-latitudes) becomes important because the introduction of genotypes with suboptimal traits into novel populations may be deleterious through the effects of outbreeding depression (Philipp 1992; Conover 1998). Hypothesis generation through modeling combined with reciprocal transplant or common garden experiments will allow us to ascertain the geographic scale by which important adaptations arise. From this, we may generate appropriate conservation guidelines for stocking and other management practices that depend on knowledge of fish growth and energetic condition.

Acknowledgements

We thank two anonymous reviewers for their helpful comments. A National Science Foundation grant (NSF-EPSCoR) through the K*Star First Award program and a Creative Research Award through the Southern Illinois University Office of Research and Development supported part of this work.

References

Arnett, A.E., and Gotelli, N.J. 1999. Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's Rule. Evolution, **53**: 1180–1188.

Atkinson, D. 1994. Temperature and organism size — a biological law for ectotherms? Adv. Ecol. Res. **25**: 1–58.

Bellman, R. 1957. Dynamic programming. Princeton University Press, Princeton, N.J.

Bunnell, D.B., and Marschall, E.A. 2003. Optimal energy allocation to ovaries after spawning. Evol. Ecol. Res. **5**: 439–457.

Carlander, K.D. 1977. Handbook of freshwater fishery biology. Vol. II. Iowa State Press, Ames, Iowa.

Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviours: pre- versus postcapture constraints on size-dependent predator–prey interactions. Oikos, **76**: 368–380.

Conover, D.O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Trans. Am. Fish. Soc. **119**: 416–430.

Conover, D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. Bull. Mar. Sci. **62**: 477–493.

Conover, D.O., and Schultz, E.T. 1995. Genotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol. Evol. **10**: 248–252.

Conover, D.O., Brown, J.J., and Ehtisham, A. 1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. Can. J. Fish. Aquat. Sci. **54**: 2401–2409.

Fullerton, A.H., Garvey, J.E., Wright, R.A., and Stein, R.A. 2000. Overwinter growth and survival of largemouth bass: interactions among size, food, origin, and winter duration. Trans. Am. Fish. Soc. **129**: 1–12.

Garvey, J.E., Wright, R.A., and Stein, R.A. 1998. Overwinter growth and survival of age-0 largemouth bass: revisiting the role of body size. Can. J. Fish. Aquat. Sci. **55**: 2414–2424.

Garvey, J.E., DeVries, D.R., Wright, R.A., and Miner, J.G. 2003. Energetic adaptations along a broad latitudinal gradient: implications for widely distributed communities. Bioscience, **53**: 141–150.

Heidinger, R.C. 1999. Stocking for sport fisheries enhancement. *In* Inland fisheries management in North America. 2nd ed. *Edited by* C.C Kohler and W.A. Hubert. Am. Fish. Soc. Spec. Publ., Bethesda, Md. pp. 375–401.

Jonassen, T.M., Imsland, A.K., Fitzgerald, R., Bonga, S.W., Ham, E.V., Naevdal, G., Stefansson, M.O., and Stefansson, S.O. 2000. Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. J. Fish Biol. **56**: 279–294.

Lankford, T.E., Billerbeck, J.M., and Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-

© 2003 NRC Canada

offs with vulnerability to predation in *Menidia menidia*. Evolution, **55**: 1873–1881.

Leggett, W.C., and Carscadden, J.E. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. J. Fish. Res. Board Can. **35**: 1469–1478.

Lindsey, C.C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. Evolution, **20**: 456–465.

Ludsin, S.A., and D.R. DeVries. 1997. First-year recruitment of largemouth bass: the inter-dependency of early life stages. Ecol. Appl. **7**: 1024–1038.

MacCrimmon, H.R., and Robbins, W.H. 1975. Distribution of the black basses in North America. *In* Black bass biology and management. *Edited by* R.H. Stroud and H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 56–66.

Mangel, M., and Clark, C.W. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, N.J.

Masaki, S. 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. *In* Evolution of insect migration and diapause. *Edited by* H. Dingle. Springer Verlag, New York. pp. 72–100.

Miranda, L.E., and Hubbard, W.D. 1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Trans. Am. Fish. Soc. **123**: 80–87.

Mousseau, T.A. 1997. Ectotherms follow the converse to Bergmann's Rule. Evolution, **51**: 630–632.

Mousseau, T.A., and Roff, D.A. 1989. Adaptation to seasonality in a cricket: patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. Evolution, **43**: 1483–1496.

Munch, S.B., and Conover, D.O. 2002. Accounting for local physiological adaptation in bioenergetic models: testing hypotheses for growth rate evolution by virtual transplant experiments. Can. J. Fish. Aquat. Sci. **59**: 393–403.

Nicieza, A.G., Reiriz, L., and Brana, F. 1994. Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. Oecologia, **99**: 243–251.

Niimi, A.J., and Beamish, F.W.H. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Can. J. Zool. **52**: 447–456.

Oster, R.A. 2002. Winter and early spring mortality and lipid composition of age-0 largemouth bass at a mid latitude. M.Sc. thesis, Southern Illinois University, Carbondale, Ill.

Partridge, L., and Coyne, J.A. 1997. Bergmann's Rule in ectotherms: is it adaptive? Evolution, **51**: 632–635.

Philipp, D.P. 1992. Stocking Florida largemouth bass outside its native range. Trans. Am. Fish. Soc. **121**: 686–691.

Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. **46**: 1958–1968.

Post, J.R., and Parkinson, E.A. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology, **82**: 1040–1051.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., and Flannery, B.P. 1992. Numerical recipes in C: the art of scientific computing. Cambridge University Press, New York.

Rice, J.A., and Cochran, P.A. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology, **65**: 732–739.

Rice, J.A., Breck, J.E., Bartell, S.M., and Kitchell, J.F. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fishes, **3**: 263–275.

Roff, D.A. 1980. Optimizing development time in a seasonal environment: the "ups and downs" of clinal variation. Oecologia, **45**: 202–208.

Roff, D.A. 1986. Predicting body size with life history models. Bioscience, **36**: 316–323.

Roff, D.A. 1992. Evolution of life histories: theory and analysis. Chapman and Hall, New York.

Shul'man, G.E. 1974. Life cycles of fish. John Wiley and Sons Inc., New York.

Schultz, E.T., and Conover, D.O. 1997. Latitudinal differences on somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). Oecologia, **109**: 516–529.

Schultz, E.T., Conover, D.O., and Ehtisham, A. 1998. The dead of winter: size-dependent variation and genetic differences in seasonal mortality among Atlantic silverside (Atherinidae: *Menidia menidia*) from different latitudes. Can. J. Fish. Aquat. Sci. **55**: 1149–1157.

Shuter, B.J., and Post, J.R. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans. Am. Fish. Soc. **119**: 314–336.

Shuter, B.J., MacLean, J.A., Fry, F.E.J., and Regier, H.A. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. **109**: 1–34.

Trebitz, A.S. 1991. Timing of spawning in largemouth bass: implications of an individual-based model. Ecol. Model. **59**: 203–227.

Weatherley, A.H., and Gill, H.S. 1987. The biology of fish growth. Academic Press, London.

Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. **49**: 2196–2218.

Wright, R.A., Garvey, J.E., Fullerton, A.H., and Stein, R.A. 1999. Using bioenergetics to explore how winter conditions affect growth and consumption of age-0 largemouth bass. Trans. Am. Fish. Soc. **128**: 603–612.

© 2003 NRC Canada

Functional responses of haemocytes in the clam *Tapes philippinarum* from the Lagoon of Venice: fishing impact and seasonal variations

Valerio Matozzo, Luisa Da Ros, Loriano Ballarin, Francesca Meneghetti, and Maria Gabriella Marin

Abstract: In the last few years, the Manila clam (*Tapes philippinarum*) has been subjected to intense fishing effort in the Lagoon of Venice owing to their commercial importance. Because of the lack of data concerning fishing-induced immunomodulation in bivalves, the consequences of fishing impact on functional responses of clam haemocytes were investigated. Clams were seasonally collected from September 2000 to July 2001 from three sites: S. Angelo, a free-fishing area, and Chioggia, inside a licensed area for clam culture, in two zones characterised by fishing and non-fishing, respectively. Haematocrit, phagocytosis, Neutral Red retention time, and lysozyme and superoxide dismutase activities were evaluated. No clear fishing effect was recorded, whereas a seasonal pattern of the cell parameters analysed was revealed. Alterations in functional responses of haemocytes seem to be more closely dependent on seasonal variations in both environmental parameters and physiological status of clams than on stress caused by fishing, and they may also be related to adaptation strategies of bivalves.

Résumé : Ces dernières années, la palourde japonaise (*Tapes philippinarum*) a été, à cause de son importance commerciale, l'objet d'une pêche intense dans le lagon de Venise. Nous avons étudié les impacts de la pêche sur les réponses fonctionnelles des hémocytes des palourdes, car il y a peu d'information sur l'immunomodulation causée par la pêche chez les bivalves. Nous avons récolté des palourdes à toutes les saisons de septembre 2000 à juillet 2001 à trois endroits, une région de pêche libre à S. Angelo et une région de culture de moules réglementée par permis à Chioggia à deux sites, l'un avec pêche et l'autre sans. Nous avons évalué l'hématocrite, la phagocytose, la durée de rétention du rouge neutre, ainsi que les activités des lysozymes et de la superoxyde dismutase. Il n'y a pas d'effet net de la pêche; cependant, il existe un pattern saisonnier de variation des paramètres cellulaires étudiés. Les changements dans les réponses fonctionnelles des hémocytes semblent donc dépendre davantage des variations saisonnières des variables du milieu et de l'état physiologique des palourdes que du stress causé par la pêche; ils peuvent aussi être reliés aux stratégies adaptatives des bivalves.

[Traduit par la Rédaction]

Introduction

Bivalve haemocytes such as granulocytes and hyalinocytes are involved in many biological functions, e.g., wound and shell repair, digestion and nutrient transport, excretion, and immune defence (Cheng 1981). The presence of non-self materials in tissues stimulates cell-mediated immune responses, which mainly include an increase in the total number of circulating haemocytes and phagocytosis of foreign materials. Phagocytised particles are generally degraded by lysosomal hydrolytic enzymes within haemocytes (Lopez et al. 1997). In some cases, lytic enzymes, and lysozyme in particular, may be released into the haemolymph during phagocytosis, thus participating in inactivation of invading microbes (Cheng et al. 1975; Mohandas et al. 1985). Phagocytosis is generally associated with increased oxygen consumption (respiratory burst) and the production of reactive oxygen species (ROS), such as superoxide anion, hydrogen peroxide, and intermediate compounds with high bactericidal activity (Pipe 1992). The humoral defence reactions of bivalve haemocytes involve the production of agglutinins, opsonins, bactericidins, and cytotoxic substances (Montes et al. 1995).

In various field and experimental studies, it has been observed that many biotic and abiotic factors may alter haemocyte-dependent defence mechanisms in bivalve molluscs. In this regard, many bioassays based on the immune responses of bivalve haemocytes, such as cell viability, phagocytosis, enzymatic activities, lysosomal membrane stability, and ROS production, have all been employed in the last few years in biomonitoring studies as stress indexes, or biomarkers, to evaluate the deleterious effects of contaminants on the well-being of organisms and the quality of their habitat. For example, it has been reported that increases in the total number of circulating haemocytes may result from either

Received 3 December 2002. Accepted 31 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 25 September 2003.
J17218

V. Matozzo, L. Ballarin, and M.G. Marin.[1] Department of Biology, University of Padova, Via Ugo Bassi 58/B, 35131, Padova, Italy.
L. Da Ros and F. Meneghetti. Institute of Marine Biology, CNR, Riva 7 Martiri 1364/A, 30122, Venezia, Italy.

[1]Corresponding author (e-mail: mgmar@civ.bio.unipd.it).

 doi: 10.1139/F03-084 © 2003 NRC Canada

proliferation or movement of cells from tissues into the haemolymph, whereas a decrease in haemocyte number may be a consequence of cell lysis or reduced movement of cells from haemolymph to tissues (Pipe and Coles 1995). Reduced haemocyte number, probably resulting from the altered physiological conditions of organisms, and enhanced susceptibility to parasite infection have been found in oysters (Ford et al. 1993). A relationship between circulating haemocyte concentration and the temperature-dependent reproductive cycle of molluscs has also been found: in *Mytilus galloprovincialis* from the Lagoon of Venice, the haemocyte number was lower in summer, the spawning period, than in spring and winter (Pipe et al. 1995). In addition, xenobiotics may affect any other immune functions in bivalve molluscs, as observed after both in vitro and in vivo exposure of animals to various contaminants (Coles et al. 1995; Auffret and Oubella 1997; Matozzo et al. 2002). In a recent study, alterations of phagocytosis, lysosomal membrane stability, and superoxide dismutase and cytochrome oxidase activities were detected in haemocytes of the clam *Tapes philippinarum* after exposure to cadmium and copper, suggesting the possibility of using these cell responses as biomarkers of exposure (Matozzo et al. 2001). Antioxidant agents, such as glutathione, glyoxalase, superoxide dismutase, and catalase act against ROS-mediated toxicity. Alterations in their activities have been proposed as biochemical biomarkers to assess the toxic effects of xenobiotics in both field and laboratory conditions (Regoli and Principato 1995; Cossu et al. 2000) and to evaluate the seasonal changes in biochemical status of animals (Power and Sheehan 1996).

Given these premises, the aim of the present study was to describe the variability in defence activities in the clam *T. philippinarum* subjected to various types of fishing impact in the Lagoon of Venice. This methodological approach was chosen on the basis of the lack of data in literature concerning fishing-induced immunomodulation in bivalves. The only information about the effects of mechanical disturbance (similar to that encountered by animals in the field) on bivalve immune responses is given by an experimental laboratory study (Lacoste et al. 2002). Because of its commercial importance, *T. philippinarum* has been subjected to intense fishing effort in the Lagoon of Venice. Free exploitation throughout the whole lagoon, in spite of regulations for management, has caused progressive reductions in natural clam stocks and areas free of fishing impact are not recognisable in the lagoon. With the aim to evaluate possible effects of fishing impact on immune responses (the number of circulating haemocytes or haematocrit, phagocytic activity, lysosomal membrane stability, and lysozyme and superoxide dismutase activities) of *T. philippinarum*, clams were collected from two differently exploited zones of the lagoon: one located in the central lagoon (S. Angelo), a free-fishing area, the other in the southern lagoon (Chioggia) inside a licensed area for clam culture.

Materials and methods

Clam sampling

Clams (2.8–3.2 cm shell length) were collected using a manual rake in September 2000 and January, April, and July 2001 from two different sites in the Lagoon of Venice (Fig. 1): S. Angelo (S-F), a free-fishing area in the central lagoon (45°24.4′N latitude, 12°16.7′E longitude), in which uncontrolled fishing is practised using both manual rakes and unauthorised dredging gears; and Chioggia, a licensed area for clam culture in the southern lagoon (45°15′N latitude, 12°16.4′E longitude), where fishing is practised daily using hydraulic dredge (Chioggia fishing area, C-F). Moreover, within the Chioggia fishing area, a control subarea was delimited in which fishing was prohibited throughout the study period (Chioggia nonfishing area, C-NF). After samplings, bivalves (at least 60 specimens per site) were immediately transferred to our laboratories for analyses.

Haemolymph collection

Haemolymph (500–750 $\mu L \cdot clam^{-1}$) was collected from the anterior adductor muscle with a 1-mL plastic syringe. In haematocrit, phagocytosis, and Neutral Red retention assays, haemolymph obtained from 10 individual clams was used; in superoxide dismutase (SOD) and lysozyme assays, haemolymph was collected from five pools of clams (5 animals per pool).

Total cell count (haematocrit)

To estimate haematocrit values, an aliquot of haemolymph was mixed with an equal volume of 10 mM L-cysteine in filtered seawater (FSW), pH 7.5, to prevent clotting. Haematocrit was estimated with a Buerker haemocytometer and expressed as haemocyte number ($\times 10^6$)·mL haemolymph^{-1}.

Phagocytosis assay

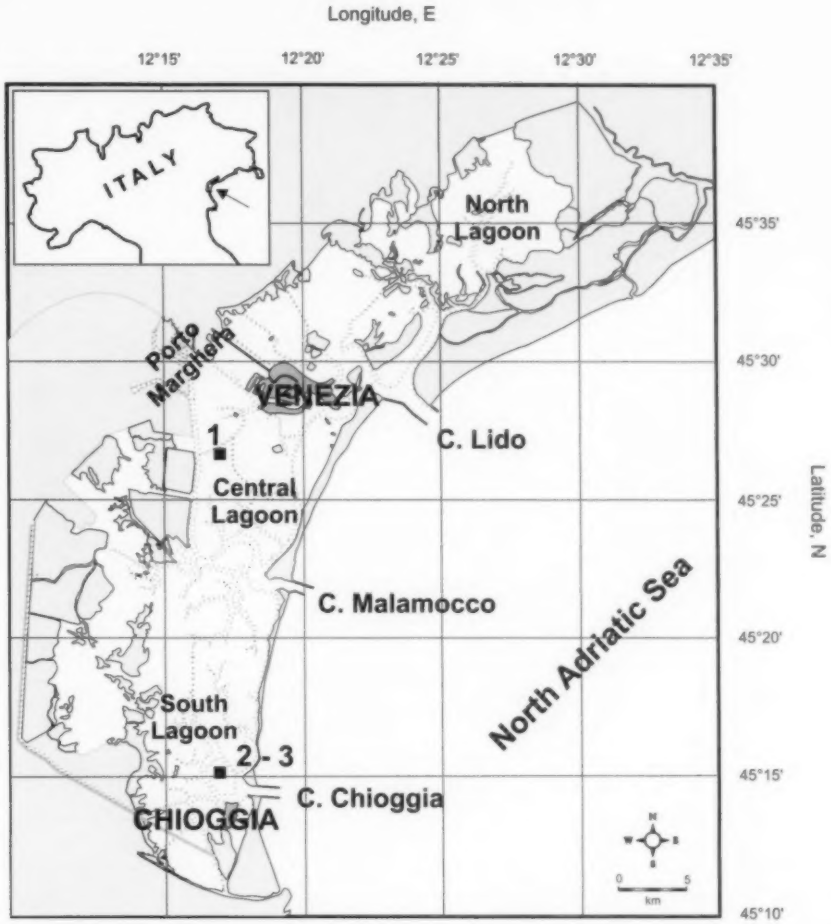
Haemolymph was placed in Eppendorf tubes containing 0.3 mL of L-cysteine and centrifuged at 780*g* for 10 min. Haemocytes were resuspended in FSW at final concentrations of 10^6 cells·mL^{-1} to prepare short-term cell cultures, according to Ballarin et al. (1994). After adhesion of haemocytes to slides, FSW was discarded from culture chambers and replaced with equal volumes of a suspension of yeast (*Saccharomyces cerevisiae*) in FSW (10:1 yeast-to-haemocyte ratio). Monolayers were incubated for 60 min at 25 °C, washed several times in FSW to eliminate uningested yeast cells, and fixed in a solution of 1% glutaraldehyde (Fluka) and 1% sucrose in FSW at 4 °C for 30 min. They were then washed in 0.1 M phosphate buffer saline (PBS; 1.37 M NaCl, 0.03 M KCl, 0.015 M KH_2PO_4, 0.065 M Na_2HPO_4), pH 7.2, for 10 min, stained with 10% Giemsa (Fluka) for 5 min, mounted on glass slides in an aqueous medium (Acquovitrex; Carlo Erba, Milan, Italy), and observed under a Leitz Dialux 22 light microscope at a magnification of 1250×. Five hundred cells per slide were counted, and the phagocytic index was expressed as the percentage of cells containing ingested yeast particles.

Neutral Red (NR) retention assay

Lysosomal membrane stability was assessed according to the method of Lowe and Pipe (1994) and Ringwood et al. (1998). Haemocyte suspension (50 µL) in 10 mM L-cysteine from individual clams was placed on microscope slides and incubated at 10 °C for 30 min in a lightproof humidity chamber to allow cells to adhere to microscope slides. A

© 2003 NRC Canada

Fig. 1. The sampling sites in the Lagoon of Venice: site 1, S. Angelo della Polvere (S-F); sites 2 and 3, concession area of Chioggia (C-F and C-NF).



stock solution of 20 mg Neutral Red (NR) dye in 1 mL dimethyl sulfoxide (DMSO) was prepared. A working solution was obtained by diluting 10-µL stock solution in 5-mL FSW. After adhesion of haemocytes, 50 µL of the NR working solution was added and coverslips were applied. After incubation, slides were observed at 15-min intervals under a light microscope, and dye loss from lysosomes into the cytosol was determined. The test was considered concluded when 50% of the small granular haemocytes exhibited NR dye spread into the whole cytosol (Lowe and Pipe 1994; Ringwood et al. 1998).

Superoxide dismutase (SOD) assay

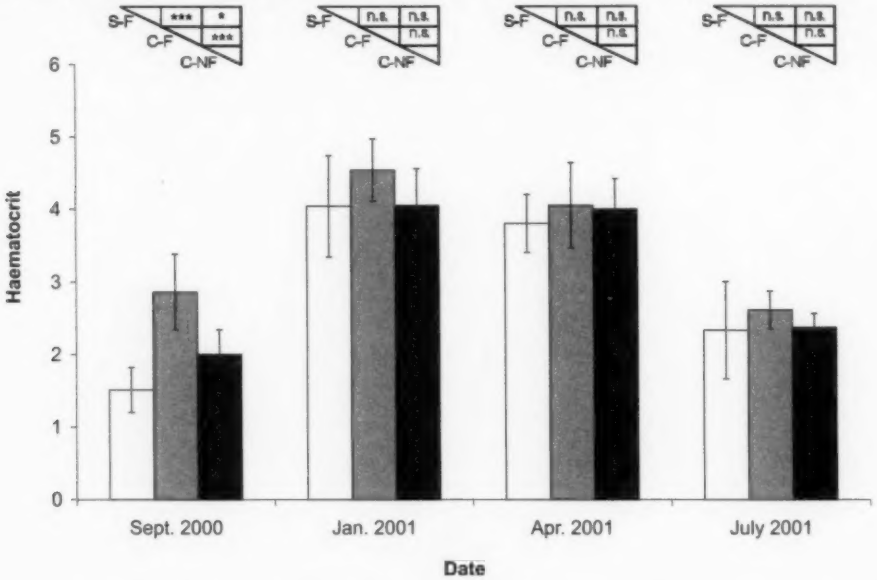
Haemolymph, collected as described above but without L-cysteine, was centrifuged at 780*g* for 10 min, and the resulting pellets were resuspended in 1 mL of distilled water. Haemocytes were then sonicated for 3 min at 0 °C with a Braun Labsonic U sonifier (Braun Biotech International, Melsunger, Germany) at 50% duty cycles and centrifuged at 12 000*g* for 30 min at 4 °C. Supernatant, called cell lysate (CL), was collected for SOD assay. SOD activity was measured following the reduction of cytochrome *c* by superoxide radical (O_2^-) generated by the xanthine – xanthine oxidase system (modified after Flohé and Ötting 1984). Cell lysate (50 µL) was added to 900 µL of solution A (5 µM xanthine in 1 mM NaOH, 2 µM cytochrome *c*, 0.1 mM EDTA (ethylene diamine tetraacetic acid) in 50 mM phosphate buffer, pH 7.8) and to 50 µL of solution B (0.45 U xanthine oxidase, 1 mL 0.1 mM EDTA in 50 mM phosphate buffer, pH 7.8). Changes in absorbance were measured at 550 nm with an Uvikon 930 spectrophotometer (Kontron Instruments, Milan, Italy). One unit of SOD is defined as the amount of enzyme inhibiting the reduction of cytochrome *c* by 50% (Flohé and Ötting 1984). Protein concentration in cell lysate was quantified according to Bradford (1976) using bovine serum albumin (BSA) as standard.

Lysozyme assay

Lysozyme activity was quantified spectrophotometrically according to the method of Fisher et al. (1996). CL (50 µL) was added to 950 µL of a 0.15% suspension of *Micrococcus lysodeikticus* (Sigma-Aldrich Corp., St. Louis, Mo.) in 66 mM

© 2003 NRC Canada

Fig. 2. Haematocrit values, expressed as number of haemocytes ($\times 10^6$)·mL^{-1} of haemopymph, in *T. philippinarum*. Values are means ± standard deviation. Open bars, S. Angelo (S-F); shaded bars, Chioggia fishing area (C-F); solid bars, Chioggia nonfishing area (C-NF). Significance of comparisons between sites is reported in the triangular matrices at the top of the figure. Asterisks indicate significant difference (Mann–Whitney *U* test, *p* values after Bonferroni adjustment): n.s., not significant; *, $p = 0.0125$; ***, $p = 2.5 \times 10^{-4}$.



phosphate buffer, pH 6.2, and the decrease in absorbance was continuously recorded at 450 nm for 5 min at 20 °C. Standard solutions containing 1, 2.5, 5, and 10 µg hen egg white lysozyme·mL phosphate buffer^{-1} were prepared (Sigma-Aldrich Corp.). The average decrease in absorbance per minute was determined for each enzyme solution, and a standard curve of enzyme concentration versus the reaction rate was drawn. One unit of lysozyme was defined as equivalent to 1 µg of lysozyme in the conditions described above. Results are expressed as U lysozyme·mg protein^{-1}. Protein concentration in cell lysate was quantified according to Bradford (1976) using BSA as standard.

Statistical analysis

For all indices, data were tested for normal distribution (Shapiro–Wilk test) and homogeneity of variances (Bartlett's test). As analysis of variance (ANOVA) assumptions were not fulfilled, the nonparametric Mann–Whitney *U* test was used to perform pairwise comparisons between samples. To correct for the four monthly comparisons, the Bonferroni adjustment was applied (Sokal and Rohlf 2000). To establish and quantify possible correlations among the variables in our data set, a multivariate analysis, principal component analysis (PCA), was performed using a matrix made of the mean values of the cell parameters measured in each site/season condition. Owing to the lack of data from two seasons in the C-NF site, NR retention values were not included in this analysis. The data matrix was used to obtain a correlation matrix from which eigenvalues and eigenvectors were extracted. The eigenvectors are independent (orthogonal) basis functions, or modes of the data, which depend on the natural coordinate of the data. The eigenvalues represent the fraction of variance contributed by each eigenvector. After varimax rotation, PCA results were displayed graphically using a biplot, which allows projection onto the plain spanned by the first two principal components of both variables (indices) and objects (samples). For all statistical analyses, the software package STATISTICA 5.5 (StatSoft, Tulsa, Okla.) was used.

Results

Clams collected at C-F showed the highest values of haematocrit and phagocytic index during the period of study. However, the haematocrit was significantly different ($p \leq 2.5 \cdot 10^{-4}$) with respect to that of clams from S-F and C-NF only in September; in the same period, significant differences ($p \leq 0.0125$) between S-F and C-NF clams were also observed (Fig. 2).

Statistically significant differences in phagocytic activity were observed in C-F clams sampled in September ($p \leq 0.0125$ vs. C-NF), January ($p \leq 0.0125$ vs. S-F), April ($p \leq 0.0125$ vs. S-F), and July ($p \leq 2.5 \cdot 10^{-4}$ vs. S-F and C-NF). A significant difference in phagocytic activity was also found between clams from S-F and C-NF in January, April, and July ($p \leq 0.0125$) (Fig. 3).

Clams from S-F showed a lower NR retention mean time compared with that of clams from C-F in September and January ($p \leq 2.5 \cdot 10^{-4}$ and $p \leq 0.0125$, respectively), whereas no statistically significant differences was observed in dye retention time among clams collected at all sampling sites in April and July (Figs. 4, 5).

No differences were found in lysozyme activity among bivalves from different sites sampled in September and July, whereas in January, enzyme activity was significantly higher ($p \leq 0.0125$) in the haemocytes of clams collected at S-F

© 2003 NRC Canada

Fig. 3. Phagocytic index, expressed as percentage of haemocytes containing ingested yeast particles, in *T. philippinarum*. Values are means ± standard deviation. Open bars, S. Angelo (S-F); shaded bars, Chioggia fishing area (C-F); solid bars, Chioggia nonfishing area (C-NF). Significance of comparisons between sites is reported in the triangular matrices at the top of the figure. Asterisks indicate significant difference (Mann–Whitney *U* test, *p* values after Bonferroni adjustment): n.s., not significant; *, $p = 0.0125$; ***, $p = 2.5 \times 10^{-4}$.

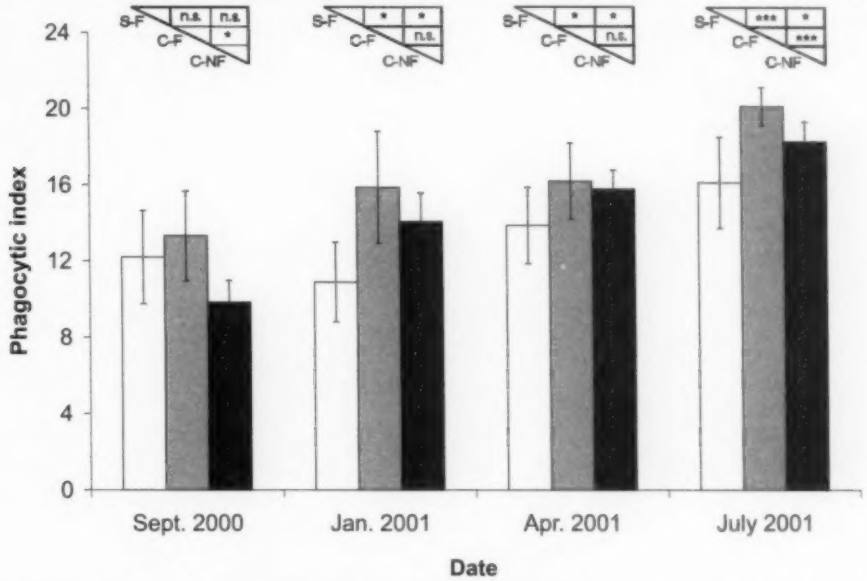
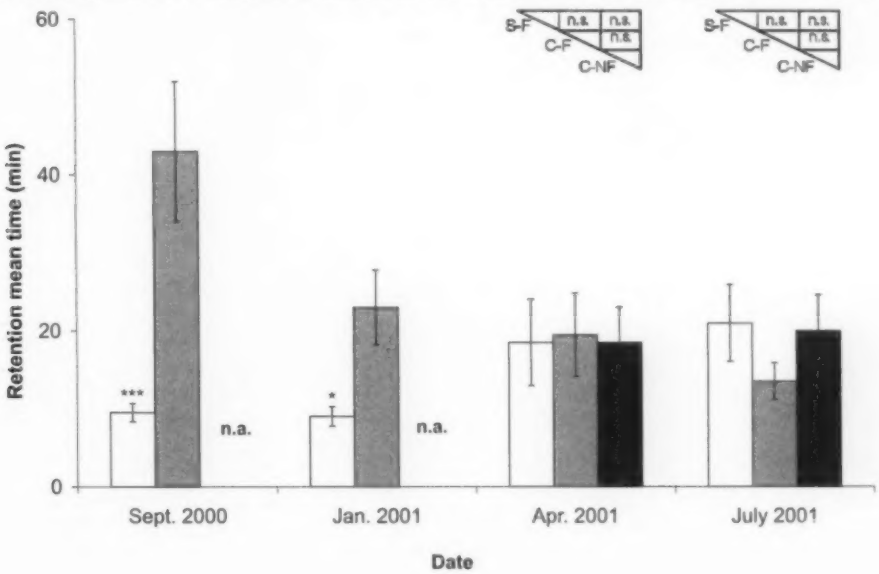


Fig. 4. Neutral Red retention time in *T. philippinarum*. Values are means ± standard deviation. Open bars, S. Angelo (S-F); shaded bars, Chioggia fishing area (C-F); solid bars, Chioggia nonfishing area (C-NF). Asterisks indicate significant difference (Mann–Whitney *U* test, *p* values after Bonferroni adjustment): n.a., data not available; n.s., not significant; *, $p = 0.0125$; ***, $p = 2.5 \times 10^{-4}$. For April and July 2001, significance of comparisons between sites is reported in the triangular matrices at the top of the figure.



compared with C-F and C-NF samples and in April in haemocytes of molluscs from C-F ($p \leq 0.0125$) compared with S-F clams (Fig. 6). Changes in SOD activity observed in clams collected in September and January at all sampling sites did not differ, whereas enzyme activity was significantly higher ($p \leq 0.0125$) in specimens collected at C-F in April and at C-NF in July (Fig. 7).

A seasonal pattern in the cell parameters analysed is also observed. Clams collected at all sampling sites showed the highest values of haematocrit and phagocytic index in Janu-

© 2003 NRC Canada

Fig. 5. *Tapes philippinarum* haemocytes stained (*a*) with Giemsa's dye containing phagocytised yeast cells (arrows) and (*b*) in vivo with Neutral Red showing obvious lysosomes (arrows) and (*c*) red cytosol. Bar length, 3 μm.

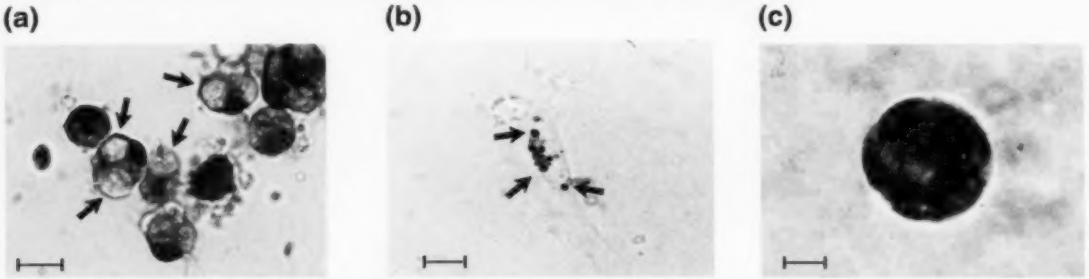
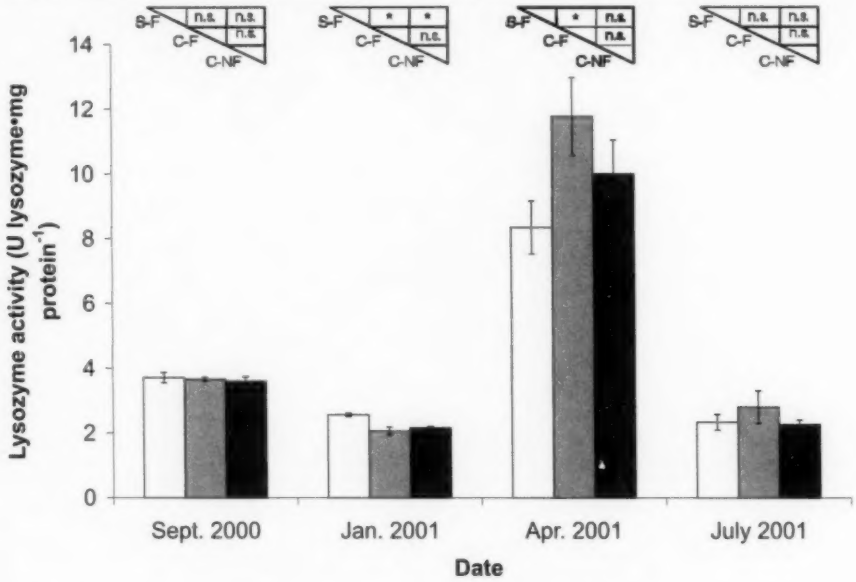


Fig. 6. Lysozyme activity, expressed as units (U) lysozyme·mg protein^{-1}, in *T. philippinarum*. Values are means ± standard deviation. Open bars, S. Angelo (S-F); shaded bars, Chioggia fishing area (C-F); solid bars, Chioggia nonfishing area (C-NF). Significance of comparisons between sites is reported in the triangular matrices at the top of the figure. Asterisks indicate significant difference (Mann–Whitney *U* test, *p* values after Bonferroni adjustment): n.s., not significant; *, $p = 0.0125$.



ary and July, respectively, whereas the highest lysozyme and SOD activities were observed in haemocytes of clams collected on April and July, respectively. A seasonal trend in NR retention mean time was only found in clams from the C-F area, values being significantly higher in autumn (retention mean time = 43 min) and lower in summer (retention mean time = 13.5 min).

In the multivariate analysis (Fig. 8), PC1 and PC2 explain over 80% of the total variance in the matrix data. The PC1 explains 46% of the total variance and is characterised by the high loadings of the variables phagocytosis and SOD (0.93 and 0.96, respectively), whereas PC2 explains 34% of the total variance, haematocrit and lysozyme showing higher loading values (0.85 and 0.80, respectively). The distribution of the various samples highlights a clear seasonal pattern; however, within each seasonal group of samples, a gradient from SF to CF can be observed. The gradients in January and July groups are mainly influenced by PC1, whereas both components are likewise responsible for the spatial distribution of the samples within April and September groups.

According to our preliminary evaluation of the data matrix, in the biplot, highest values of phagocytic and SOD activity appear associated mostly with July samples, haematocrit and lysozyme activity with April samples.

Discussion

The main objective of this study was to analyse possible changes in cell parameters of *T. philippinarum* subjected to stress induced by fishing in the Lagoon of Venice. However, the results obtained demonstrate that functional responses of haemocytes exhibit seasonal patterns that may be related to changes in physical, chemical, and biological factors occurring at all sampling sites in the study period. Generally, bivalves collected at S. Angelo (free-fishing area) showed a reduction in immune responses with respect to clams from

© 2003 NRC Canada

Fig. 7. Superoxide dismutase (SOD) activity, expressed as units (U) SOD·mg protein^{-1}, in *T. philippinarum*. Values are means ± standard deviation. Open bars, S. Angelo (S-F); shaded bars, Chioggia fishing area (C-F); solid bars, Chioggia nonfishing area (C-NF). Significance of comparisons between sites is reported in the triangular matrices at the top of the figure. Asterisks indicate significant difference (Mann–Whitney *U* test, *p* values after Bonferroni adjustment): n.s., not significant; *, $p = 0.0125$.

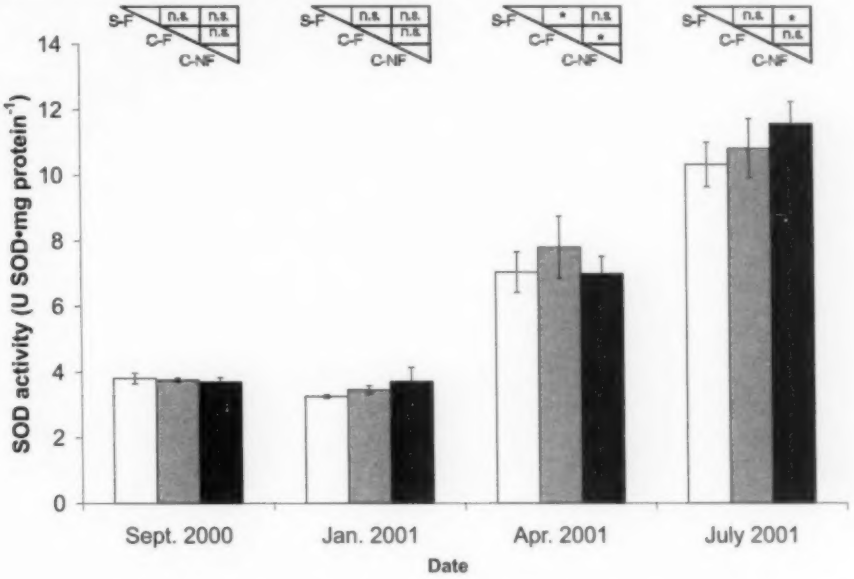
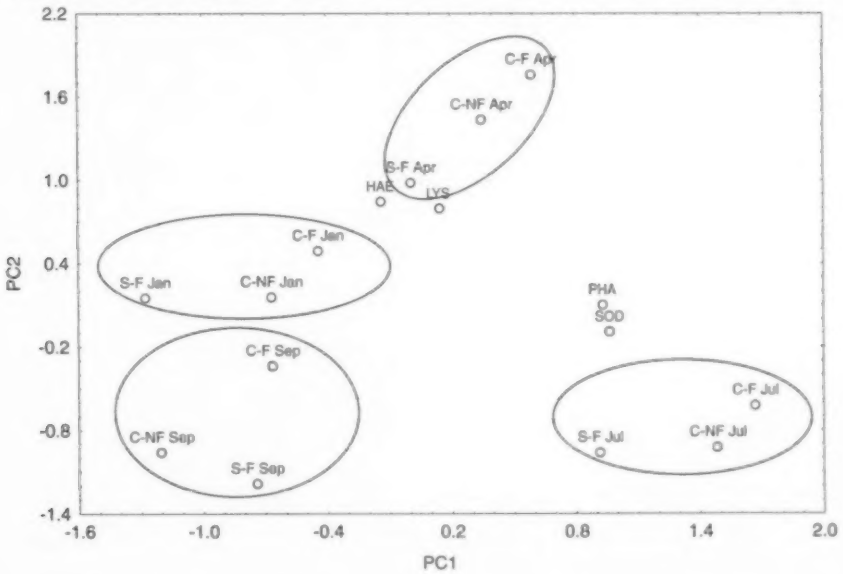


Fig. 8. Principal component analysis (PCA) for seasonal (January, Jan; April, Apr; July, Jul; September, Sep) clam samples from three sites (S. Angelo, S-F; Chioggia fishing area, C-F; Chioggia nonfishing area, C-NF). The four variables considered are haematocrit value (HAE), phagocytic activity (PHA), lysozyme activity (LYZ), and superoxide dismutase activity (SOD).



Chioggia (licensed area). In particular, the highest values of both total haemocyte number and phagocytic index observed in animals collected in the Chioggia fishing area (C-F) suggest more efficient immunosurveillance of these animals. However, our data also reveal the lack of any direct or indirect prevalent influence of the fishing on haemocyte functional responses, the C-F area being subjected to this activity, as probably occurs at S-F.

As already reported, significant differences in haematocrit values were only found in September, whereas the phagocytic index varied greatly throughout the year. The haematocrit was probably affected by seasonal changes in

© 2003 NRC Canada

physiological factors, mostly related to the reproductive cycle, haemocyte number being lower in clams collected in September 2000 and July 2001, presumably in postspawning conditions. In this regard, *T. philippinarum* from the same sampling areas showed two spawning periods in the early summer (June) and late summer (August) (L. Da Ros, unpublished data). A similar seasonal pattern in circulating haemocyte number was also found in *M. galloprovincialis* from the Lagoon of Venice (Pipe et al. 1995) and from Ría de Vigo, Spain (Santarém et al. 1994), and in *Crassostrea virginica* from Apalachicola Bay, Florida (Fisher et al. 1996). Probably, a mobilisation of haemocytes towards gonads occurs to remove cell debris remaining after spawning, as proposed by Suresh and Mohandas (1990). Moreover, reductions in haematocrit values during summer 2000 and autumn 2001 may also be associated with haemocyte infiltration into clam tissues to respond to parasites, which are generally known to exhibit higher densities when higher water temperatures are reached. In the study areas, many haemocytes were observed inside gonads in late summer – autumn 2001 when high parasitic body burdens (*Perkinsus* sp.) were also found, particularly in clams from Chioggia (L. Da Ros, unpublished data). Decreased haemocyte concentrations with the increasing presence of pathogens were also observed in *Ruditapes philippinarum* after 7 weeks of experimental challenge with *Vibrio* P1 (Oubella et al. 1994).

In cell-mediated immune responses, phagocytosis by circulating haemocytes is the main defence against pathogens and foreign materials (Cheng 1981). Generally, phagocytic activity was significantly reduced in clams collected at S. Angelo, suggesting immune suppression to which several factors may contribute. Although reasons are uncertain, it is probable that fishing causes a stress syndrome affecting the functional responses of clam haemocytes, as observed in *C. gigas* subjected to experimental mechanical disturbance (Lacoste et al. 2002). However, the highest phagocytic index, as well as haematocrit values, observed in clams from the Chioggia fishing area hinders overall evaluation of results. In this area, characterised by recurrent displacement of clams from one site to another and introduction from other sites of the Lagoon, we hypothesise that animals may enhance phagocytic activity to adapt their physiological responses to changing environmental conditions. Increased immune responses in clams from C-F may be due to compensation following the reduction in immune surveillance previously suffered, in agreement with the hypothesis of Lacoste et al. (2002). Moreover, the central basin of S. Angelo is adversely affected by higher pollution levels, arising from both untreated municipal sewage from the city of Venice and effluents from the nearby industrial area of Porto Marghera, with consequent homogeneous spatial distribution of a wide range of organic and inorganic contaminants, polychlorinated biphenyls (PCBs), and heavy metals in particular (Frignani et al. 2001*a*, 2001*b*). Sediment mobilisation, due to dredging and passage of ships, may cause resuspension of contaminants (Frignani et al. 2001*a*), which in turn may affect the physiological responses of clams. Several in vitro and in vivo laboratory studies have demonstrated that phagocytosis may be affected by exposure to xenobiotics (Coles et al. 1994; Cima et al. 1998; Matozzo et al. 2001). In field conditions, Sami et al. (1992) and Pipe et al. (1995) observed reduced phagocytic activity in molluscs from contaminated sites compared with that of bivalves from reference sites. In the present study, phagocytosis also showed similar seasonal fluctuations at all sampling sites, demonstrating that other seasonally variable factors, such as gametogenic cycle and parasitosis, are mostly involved in regulating immunocompetence in clams.

Generally, clams from S. Angelo showed reduced NR retention mean times (from 9.5 to 21 min) with respect to molluscs from Chioggia (up to 43 min), particularly in autumn–winter. These results are similar to those obtained in *M. galloprovincialis* from both moderately (from 20 to 30 min) and highly (from 5 to 10 min) polluted areas of the lagoon (Lowe et al. 1995). However, values recorded in Chioggia animals were lower than those reported for *M. galloprovincialis* from the same area (up to 120 min) (Lowe et al. 1995), demonstrating that lysosomes of haemocytes in *T. philippinarum* may retain NR dye for a shorter time than those of *M. galloprovincialis* (Lowe et al. 1995), in agreement with the results of Matozzo et al. (2001).

No clear fishing impact was observed on the enzymatic activities of clams, lysozyme and SOD being highly variable in specimens from all sites throughout the study period. Lysozyme is one of the most important bacteriolytic agents against several species of Gram-positive and Gram-negative bacteria, which may be secreted by haemocytes into the haemolymph during phagocytosis (Cheng et al. 1975). The highest and lowest lysozyme activities were found in clams collected at all sampling sites in April and July, respectively, in contrast with the results of other studies, in which the highest lysozyme activity was observed in bivalve haemolymph in summer (Santarém et al. 1994; Fisher et al. 1996). However, these different results may be due to the experimental procedures used to measure lysozyme activity. We determined enzyme activity in cell lysate, because in our previous observations, higher lysozyme levels were found in haemocytes than in haemolymph of *T. philippinarum*, in agreement with the results of Carballal et al. (1997) and Lopez et al. (1997). Therefore, low lysozyme activity during summer may be explained by increased enzyme secretion from haemocytes in the haemolymph as a consequence of higher phagocytosis probably caused by enhanced bacterial activity during this period. A relationship between lysozyme and phagocytic activity may also be highlighted, phagocytosis being higher in July.

Antioxidants may maintain ROS at relatively low levels, reducing cell damage such as lipid peroxidation. Although SOD activity varied irregularly in analysed clams throughout the year, this pattern seems to be more closely related to seasonal changes in biochemical components of haemolymph than to the impact of fishing. In clams collected from all sampling sites, a significant reduction in SOD occurred during winter, whereas the highest values were found during summer. This may be due to the influence of factors that generally show seasonal fluctuations, such as temperature, oxygen, salinity, availability of food, and xenobiotics (Baumard et al. 1999; Gómez-Ariza et al. 2000). With regard to this, the highest values of temperature were recorded in summer (27 °C in July at S. Angelo, 26 °C in June at Chioggia) and the lowest in winter (5 and 3 °C in January at S. Angelo and Chioggia, respectively), whereas salinity ranged from 34‰

© 2003 NRC Canada

to 27.7‰ at S. Angelo and from 37.1‰ to 23.3‰ at Chioggia. However, the reproductive period, which occurs from spring to autumn in *T. philippinarum*, may be considered responsible for the enhanced metabolic activity of animals, followed by increases in both oxygen consumption and ROS production and, consequently, increased antioxidant activities. SOD levels were also low throughout the autumn–winter months, increasing in spring up to a maximum in June in *M. galloprovincialis* (Viarengo et al. 1991). Seasonal patterns of antioxidant defences were also found to be closely related to seasonal variations in temperature and reproductive cycle in the brown mussel *Perna perna* (Filho et al. 2001) and the oyster *Saccostrea cucullata* (Niyogi et al. 2001). In agreement with the hypothesis of Regoli (1998), increased SOD activity during the reproductive period is related to the higher metabolic status of organisms during spawning and (or) to the need for more efficient protection against ROS-mediated damage during this phase.

In conclusion, alterations in the functional responses of haemocytes of *T. philippinarum* observed in the present work seem to be more closely dependent on seasonal variations in both environmental parameters (food availability, temperature, oxygen, salinity, etc.) and physiological status of clams (gametogenic cycle) than on stress caused by fishing impact in the Lagoon of Venice. In particular, a similar pattern can be shown for both phagocytic and SOD activity indices and condition index values, as reported by Marin et al. (2003) in clams collected in the same period and sites. In clams from S. Angelo, lower values of analysed cell parameters were often found, perhaps as a consequence of fishing impact. However, high values in both haematocrit and phagocytic index detected in clams from the Chioggia fishing area demonstrate that alterations in haemocyte responses may also be related to adaptation strategies. *Tapes philippinarum* collected from other zones of the lagoon are repeatedly introduced by fishermen into the fishing grounds of the clam farms to balance clams harvested for commercial purpose. This situation presumably results in increases of functional responses of haemocytes to adapt clam physiological performances to changing environmental conditions. On the whole, it is suggested that the influence of many endogenous and exogenous factors needs to be more fully investigated to facilitate evaluation of possible detrimental effects of fishing on the functional responses of haemocytes.

Acknowledgements

This work was supported by a grant from the European Union (Studies 99/062: Assessing the impact of bivalve fisheries on the benthic ecosystems of the Ria Formosa Lagoon (Portugal), Venice Lagoon (Italy), Aegean Sea (Kavala-Greece) and on the juvenile flatfish in the south coast of Portugal (IMPACTO)). The authors are grateful to Dr. Marco Montanari for his assistance in performing statistical analysis.

References

Auffret, M., and Oubella, R. 1997. Hemocyte aggregation in the oyster *Crassostrea gigas*: *in vitro* measurement and experimental modulation by xenobiotics. Comp. Biochem. Physiol. A, **118**: 705–712.

Ballarin, L., Cima, F., and Sabbadin, A. 1994. Phagocytosis in the colonial ascidian *Botryllus schlosseri*. Dev. Comp. Immunol. **18**: 467–481.

Baumard, P., Budzinski, H., Garrigues, P., Dizer, H., and Hansen, P.D. 1999. Polycyclic aromatic hydrocarbons in recent sediments and mussels (*Mytilus edulis*) from the western Baltic Sea: occurrence, bioavailabilty and seasonal variations. Mar. Environ. Res. **47**: 17–47.

Bradford, M.M. 1976. A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of the protein–dye binding. Anal. Biochem. **72**: 248–254.

Carballal, M.J., Lopez, C., Azevedo, C., and Villalba, A. 1997. Enzymes involved in defense functions of hemocytes of mussel *Mytilus galloprovincialis*. J. Invertebr. Pathol. **70**: 96–105.

Cheng, T.C. 1981. Bivalves. *In* Invertebrate blood cells — 1. *Edited by* N.A. Ratcliffe and A.F. Rowley. Academic Press, London. pp. 233–300.

Cheng, T.C., Rodrick, G.E., Foley, D.A., and Koehler, S.A. 1975. Release of lysozyme from hemolymph cells of *Mercenaria mercenaria* during phagocytosis. J. Invertebr. Pathol. **25**: 261–265.

Cima, F., Marin, M.G., Matozzo, V., DaRos, L., and Ballarin, L. 1998. Immunotoxic effects of organotin compounds in *Tapes philippinarum*. Chemosphere, **37**: 3035–3045.

Coles, J.A., Farley, S.R., and Pipe, R.K. 1994. Effects of fluoranthene on the immunocompetence of the common marine mussel, *Mytilus edulis*. Aquat. Toxicol. **30**: 367–379.

Coles, J.A., Farley, S.R., and Pipe, R.K. 1995. Alteration of the immune response of the common marine mussel *Mytilus edulis* resulting from exposure to cadmium. Dis. Aquat. Org. **22**: 59–65.

Cossu, C., Doyotte, A., Babut, M., Exinger, A., and Vasseur, P. 2000. Antioxidant biomarkers in freshwater bivalves, *Unio tumidus*, in response to different contamination profiles of aquatic sediments. Ecotoxicol. Environ. Saf. **45**: 106–121.

Filho, D.W., Tribess, T., Gaspari, C., Claudio, F.D., Torres, M.A., and Magalhães, A.R.M. 2001. Seasonal changes in antioxidant defenses of the digestive gland of the brown mussel (*Perna perna*). Aquaculture, **203**: 149–158.

Fisher, W.S., Oliver, L.M., and Edwards, P.E. 1996. Hematologic and serologic variability of eastern oysters from Apalachicola Bay, Florida. J. Shellfish Res. **15**: 554–564.

Flohé, L., and Ötting, F. 1984. Superoxide dismutase assays. Methods Enzymol. **105**: 93–104.

Ford, S.E., Kanaley, S.A., and Littlewood, D.T.J. 1993. Cellular responses of oysters infected with *Haplosporidium nelsoni*: changes in circulating and tissue-infiltrating hemocytes. J. Invertebr. Pathol. **61**: 49–57.

Frignani, M., Bellucci, L.G., Carraro, C., and Raccanelli, S. 2001*a*. Polychlorinated biphenyls in sediments of the Venice Lagoon. Chemosphere, **43**: 567–575.

Frignani, M., Bellucci, L.G., Carraro, C., and Favotto, M. 2001*b*. Accumulation of polychlorinated dibenzo-*p*-dioxins and dibenzofurans in sediments of the Venice Lagoon and the industrial area of Porto Marghera. Mar. Pollut. Bull. **42**: 544–553.

Gómez-Ariza, J.L., Giràldez, I., and Morales, E. 2000. Temporal fluctuations of tributyltin in the bivalve *Venerupis decussata* at five stations in Southwest Spain. Environ. Pollut. **108**: 279–290.

Lacoste, A., Malham, S.K., Gélébart, F., Cueff, A., and Poulet, S.A. 2002. Stress-induced immune changes in the oyster *Crassostrea gigas*. Dev. Comp. Immunol. **26**: 1–9.

Lopez, C., Carballal, M.J., Azevedo, C., and Villalba, A. 1997. Enzyme characterisation of the circulating haemocytes of the carpet shell clam, *Ruditapes decussatus* (Mollusca: Bivalvia). Fish Shellfish Immunol. **7**: 595–608.

© 2003 NRC Canada

Lowe, D.M., and Pipe, R.K. 1994. Contaminant induced lysosomal membrane damage in marine mussel digestive cells: an in vitro study. Aquat. Toxicol. **30**: 357–365.

Lowe, D.M., Fossato, V.U., and Depledge, M.H. 1995. Contaminant-induced lysosomal membrane damage in blood cells of mussels *Mytilus galloprovincialis* from the Venice Lagoon: an *in vitro* study. Mar. Ecol. Progr. Ser. **129**: 189–196.

Marin, M.G., Moschino, V., Deppieri, M., and Lucchetta L. 2003. Variations in gross biochemical composition, energy value and condition index of *T. philippinarum* from the Lagoon of Venice. Aquaculture, **219**: 859–871.

Matozzo, V., Ballarin, L., Pampanin, D.M., and Marin, M.G. 2001. Effects of copper and cadmium exposure on functional responses of hemocytes in the clam, *Tapes philippinarum*. Arch. Environ. Contam. Toxicol. **41**: 163–170.

Matozzo, V., Ballarin, L., and Marin, M.G. 2002. *In vitro* effects of tributyltin on functional responses of haemocytes in the clam *Tapes philippinarum*. Appl. Organomet. Chem. **16**: 169–174.

Mohandas, A., Cheng, T.C., and Cheng, J.B. 1985. Mechanism of lysosomal enzyme release from *Mercenaria mercenaria* granulocytes: a scanning electron microscope study. J. Invertebr. Pathol. **45**: 189–197.

Montes, J.F., Durfort, M., and Garcia-Valero, J. 1995. Cellular defence mechanism of the clam *Tapes semidecussatus* against infection by the protozoan *Perkinsus* sp. Cell Tissue Res. **279**: 529–538.

Niyogi, S., Biswas, S., Sarker, S., and Datta, A.G. 2001. Antioxidant enzymes in brackishwater oyster, *Saccostrea cucullata*, as potential biomarkers of polyaromatic hydrocarbon pollution in Hooghly Estuary (India): seasonality and its consequences. Sci. Total Environ. **281**: 237–246.

Oubella, R., Paillard, C., Maes, P., and Auffret, M. 1994. Changes in hemolymph parameters in the Manila clam *Ruditapes philippinarum* (Mollusca, Bivalvia) following bacterial challenge. J. Invertebr. Pathol. **64**: 33–38.

Pipe, R.K. 1992. Generation of reactive oxygen metabolites by the haemocytes of the mussel *Mytilus edulis*. Dev. Comp. Immunol. **16**: 111–122.

Pipe, R.K., and Coles, J.A. 1995. Environmental contaminants influencing immune function in marine bivalve molluscs. Fish Shellfish Immunol. **5**: 581–595.

Pipe, R.K., Coles, J.A., Thomas, M.E., Fossato, V.U., and Pulsford, A.L. 1995. Evidence for environmentally derived immunomodulation in mussels from the Venice Lagoon. Aquat. Toxicol. **32**: 59–73.

Power, A., and Sheehan, D. 1996. Seasonal variation in the antioxidant defence systems of gill and digestive gland of the blue mussel, *Mytilus edulis*. Comp. Biochem. Physiol. C, **114**: 99–103.

Regoli, F. 1998. Trace metals and antioxidant enzymes in gills and digestive gland of the Mediterranean mussel *Mytilus galloprovincialis*. Arch. Environ. Contam. Toxicol. **34**: 48–63.

Regoli, F., and Principato, G. 1995. Glutathione, glutathione-dependent and antioxidant enzymes in mussel, *Mytilus galloprovincialis*, exposed to metals under field and laboratory conditions: implications for the use of biochemical biomarkers. Aquat. Toxicol. **31**: 143–164.

Ringwood, A.H., Conners, D.E., and DiNovo, A. 1998. The effects of copper exposures on cellular responses in oysters. Mar. Environ. Res. **46**: 591–595.

Sami, S., Faisal, M., and Huggett, R.J. 1992. Alterations in cytometric characteristics of hemocytes from the American oyster *Crassostrea virginica* exposed to a polycyclic aromatic hydrocarbon (PAH) contaminated environment. Mar. Biol. **113**: 247–252.

Santarém, M.M., Robledo, J.A.F., and Figueras, A. 1994. Seasonal changes in hemocytes and serum defense factors in the blue mussel *Mytilus galloprovincialis*. Dis. Aquat. Org. **18**: 217–222.

Sokal, R.R., and Rohlf, F.J. 2000. Biometry. W.H. Freeman and Company, New York.

Suresh, K., and Mohandas, A. 1990. Number and types of hemocytes in *Sunetta scripta* and *Villorita cyprinoides* var. *cochinensis* (Bivalvia), and leukocytosis subsequent to bacterial challenge. J. Invertebr. Pathol. **55**: 312–318.

Viarengo, A., Canesi, L., Pertica, M., and Livingstone, D. 1991. Seasonal variations in the antioxidant defence enzymes and lipid peroxidation of the digestive gland of mussels. Comp. Biochem. Physiol. C, **100**: 187–190.

© 2003 NRC Canada

Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes

P.J. Dillon, B.J. Clark, L.A. Molot, and H.E. Evans

Abstract: The optimal habitat boundary for lake trout (*Salvelinus namaycush* Walbaum) has been defined as that portion of the lake having both more than 6 mg·L^{-1} oxygen and temperature less than 10 °C. Here we use an existing hypolimnetic oxygen model to define the lower boundary of the optimal habitat by identifying the depth at which 6 mg·L^{-1} oxygen occurs at the end-of-summer stratification period. Then we develop a new model to predict the 10 °C depth or upper habitat boundary for the same date. These two boundaries can be used in conjunction with measured individual strata volumes to calculate the optimal habitat volume. Parameters needed for the models include lake morphometry, total phosphorus (TP) concentration, and Secchi depth or dissolved organic carbon (DOC) concentration. Thus, the optimal habitat model can be used to predict the effects on optimal habitat volumes of changes in trophic status (increases or decreases in TP), or changes in light transmission (caused by changes in DOC or its surrogate in these lakes, i.e., Secchi depth) that result from changes in climate, land use, acid–base status, or incident ultraviolet radiation levels.

Résumé : L'habitat optimal du touladi (*Salvelinus namaycush* Walbaum) a été défini comme la portion du lac qui possède simultanément une concentration d'oxygène supérieure à 6 mg·L^{-1} et une température inférieure à 10 °C. Nous utilisons un modèle déjà existant de l'oxygène de l'hypolimnion pour définir la frontière inférieure de l'habitat optimal en déterminant la profondeur à laquelle se situe la concentration d'oxygène de 6 mg·L^{-1} à la fin de la période de stratification estivale. Nous avons ensuite mis au point un nouveau modèle pour prédire la profondeur de la température de 10 °C, soit la frontière supérieure de l'habitat, pour la même date. Ces deux frontières combinées aux mesures des volumes des différentes strates peuvent servir à calculer le volume de l'habitat optimal. Les variables requises pour ces modèles sont la morphométrie du lac, la concentration de phosphore total (TP) et la profondeur de Secchi ou alors la concentration de carbone organique dissous (DOC). Ainsi, le modèle d'habitat optimal peut servir à prédire les effets sur le volume de l'habitat optimal de changements dans le statut trophique (accroissements ou réductions de TP) ou de changements dans la transmission de la lumière (causés par des changements dans le DOC, ou son substitut dans ces lacs, c'est-à-dire, la profondeur de Secchi) qui résultent de modifications du climat, de l'utilisation des terres, du statut acide–base ou des intensités de radiation ultraviolette incidente.

[Traduit par la Rédaction]

Introduction

Fisheries that include cold water species such as lake trout (*Salvelinus namaycush* Walbaum) are an important resource in Ontario, in the Laurentian Great Lakes (Selgeby et al. 1995), and in smaller inland lakes (Evans and Olver 1995). Examining the potential for success or failure of lake trout populations usually requires, as a minimum, a measurement of suitable habitat volumes for the lakes in question (Christie and Regier 1988; Evans et al. 1991), although Ryan and Marshall (1994) presented a rapid diagnostic method based on only mean depth and habitat quality (phosphorous, Secchi depth, chlorophyll). These fish populations generally require large volumes of cold, well-oxygenated water to thrive (Martin and Olver 1980); thus, their optimal habitat boundaries are defined by temperature (<10 °C) at the top and by oxygen (>6 mg·L^{-1}) at the bottom (Ontario Ministry of the Environment (OMOE) and Ontario Ministry of Natural Resources (OMNR) 1986; Evans et al. 1991), although there is some evidence that populations can be successful at higher temperatures under some circumstances (Snucins and Gunn 1995; Sellers et al. 1998). Because these boundaries are eas-

Received 6 June 2002. Accepted 4 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 25 September 2003.
J16929

P.J. Dillon.[1] Department of Environmental and Resource Studies, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.
B.J. Clark. Dorset Research Centre, P.O. Box 39, Dorset, ON P0A 1E0, Canada.
L.A. Molot. Faculty of Environmental Studies, York University, 4700 Keele St., Toronto, ON M3J 1P3, Canada.
H.E. Evans. RODA Environmental Reseach Ltd., P.O. Box 447, Lakefield, ON K0L 2H0, Canada.

[1]Corresponding author (e-mail: pdillon@trentu.ca).

 doi: 10.1139/F03-082 © 2003 NRC Canada

ily measured using portable field equipment (temperature–oxygen meters), they present a relatively simple means of assessing habitat suitability. The most appropriate time for these measurements is the late summer period when minimal hypolimnetic oxygen concentrations and maximum temperatures, i.e., worst-case conditions with respect to lake trout habitat, usually are found in dimictic lakes (Evans et al. 1991). Because of this, Evans et al. (1991) used habitat volumes "standardized" to 31 August and Molot et al. (1992) standardized end-of-summer oxygen profiles to 1 September. The ability to estimate long-term mean habitat volume, as well as typical ranges between years, would be useful for resource managers who oversee the management of many lake trout lakes for which long-term data are not available.

Existing optimal habitat models acknowledge the link between habitat volume and some measure of both lake morphometry and trophic status. For example, the optimal habitat model used for lake trout management in inland lakes in southeastern Ontario (OMOE and OMNR 1993) uses mixing ratios and mean summer chlorophyll *a* to estimate the proportion of the habitat that is optimal. Fee et al. (1996) found that mixing depths (which have a strong effect on the determination of upper habitat boundaries) were best identified using extinction coefficients (converted to percent transmission), which principally are functions of dissolved organic carbon (DOC) except in those cases in which algal levels are high (i.e., eutrophic lakes). These parameters, however, are costly to measure and are rarely collected with enough frequency to establish ice-free mean values with good precision. In addition, models that predict percent optimal habitat offer no specific information about the location of habitat boundaries defined by temperature and oxygen. Proportional volumes alone cannot provide information regarding how environmental change might affect the habitat boundaries. For example, determining the effect of increasing transparency on habitat volumes is of interest because of recent work linking climate change, as well as other regional-scale stresses such as acid rain, to changes in transparency (Fee et al. 1996; Molot and Dillon 1997; Schindler 1997).

For the above reasons, we propose the use of two simple models to estimate long-term average optimal habitat boundaries for lake trout defined by both temperature and oxygen criteria. A hypolimnetic oxygen profile model (Molot et al. 1992; Clark et al. 2002) can be used to define the mean long-term lower boundary ($Z_{6\ mg \cdot L^{-1}}$) of the optimal habitat. Because this model uses lake morphometry and total phosphorus (TP) to predict hypolimnetic oxygen profiles for the late summer period (1 September), it can be used to estimate the depth of the specific O_2 concentration of interest (here we use 6 $mg \cdot L^{-1}$). In this paper, we develop a model to predict the depth at which 10 °C occurs (Z_{10}) at the same late summer time. Because there is substantial published information indicating that temperature profiles and mixing depths are governed by some measure of lake size and by water transparency (Fee et al. 1996), we focus on DOC and Secchi depth, two measures of transparency that are collected routinely, as well as various lake morphometry parameters, as independent variables in a temperature model. These two modelled boundary depths can then be combined with measured morphometric data (strata volumes) to calculate long-term optimal lake trout habitat volumes standardized to a specific time, the end of summer (1 September). Although the two models represent near worst-case conditions with respect to habitat volume, the combined models can be used to predict the effects of changes in trophic status or transparency on the upper and lower optimal habitat boundaries for a given lake. Other oxygen and temperature criteria have been used to define other classes of lake trout habitat; for example, Evans et al. (1991) have defined "usable" habitat as that with $O_2 > 4$ $mg \cdot L^{-1}$ and temperature < 15 °C. A modelling approach analogous to what we report here could be used to define the location of these boundaries and thus define usable lake trout habitat, or any other class of habitat with defined temperature and oxygen criteria. Furthermore, should the definition or criteria defining optimal or any other category of habitat change in future, the models presented here can be easily modified to apply to any other temperature or oxygen levels desired.

Materials and methods

The lakes in the set used for development of the temperature model (lake set 1) were sampled over periods ranging from 3 to 19 years (mean 13 years). The sampling frequency within years varied among both lakes and years; for example, in Blue Chalk Lake, sampling was carried out weekly from 1976 to 1982, biweekly from 1983 to 1989, and monthly thereafter. Some of the lakes with shorter records were sampled monthly in all years. In most cases, more than 10 years of data were used to determine mean, long-term Z_{10}.

Field data collection methods have been described elsewhere (Girard and Reid 1990; Molot et al. 1992; Clark 1996). Oxygen concentrations were measured either by Winkler titration or with portable or lab-based YSI oxygen meters (YSI Inc., Yellow Springs, Ohio). Temperature measurements were made with a Flett digital telethermometer (Flett Research Ltd., Winnipeg, Man.) or with a YSI digital temperature–oxygen meter after the appropriate calibrations.

The Z_{10}s of the lakes used for developing the temperature model were standardized to 1 September for each year that the lake was sampled by establishing Z_{10} to the nearest 0.1 m on the dates immediately before and after 1 September (but not more than 14 days away) and linearly interpolating to calculate Z_{10} precisely on 1 September. The Z_{10} model was developed using stepwise multiple regression.

Sampling of lakes in the test set (lake set 2) was substantially less frequent than that for lake set 1, with an average of 10 years with data. For this set, observed mean 10 °C isotherms and 6 $mg \cdot L^{-1}$ O_2 isolines were derived from the closest dates each year to 1 September because sampling dates bracketing 1 September within 14 days were not always available.

The predicted upper and lower optimal habitat boundaries were estimated using the temperature model developed here and the hypolimnetic oxygen model described in Molot et al. (1992), respectively. The latter is a multiple regression model that has been used to predict end-of-summer oxygen concentrations at 2-m intervals in the hypolimnion. The model utilizes ratios of volumes of individual strata to sediment surface areas and total phosphorus concentration at spring overturn (TP_{so}) as inputs. It can be used to estimate spring oxygen concentrations if measurements are unavailable and uses these

© 2003 NRC Canada

Table 1. Area (A_0), mean depth ($\bar{z}$), maximum depth (z_{max}), maximum distance across lake through central basin (MD), total phosphorus (TP), Secchi depth, and dissolved organic carbon (DOC) concentration for the lakes used to develop the Z_{10} model (lake set 1).

Lake	A_0 (ha)	$\bar{Z}$ (m)	z_{max} (m)	MD (km)	TP ($\mu g \cdot L^{-1}$)	Secchi (m)	DOC (mg $C \cdot L^{-1}$)
Basshaunt	47	8	24	0.7	6.5	4.4	4.2
Big Porcupine	235	8	31	1.2	3.4	6.5	2.1
Bigwind	111	11	32	2.6	6.8	4.7	2.9
Blue Chalk	52	9	23	0.9	5.0	6.8	1.8
Bonnechere	105	6	21	1.3	4.1	5.3	3.28
Buck	40	11	30	1.2	5.7	5.9	3.2
Chub	34	9	27	1.2	8.4	3.3	4.8
Cinder	27	5	16	1.0	12.0	2.4	5.3
Cinder East	50	10	37	1.3	14.0	2.5	5.3
Clear	88	12	33	1.2	4.3	8.0	1.6
Cradle	18	12	33	0.8	5.2	8.2	1.5
Crosson	57	9	25	1.0	9.1	3.6	4.1
Crown	136	8	30	1.1	3.7	7.1	1.9
Crystal	41	4	17	0.8	4.5	6.0	3.1
Delano	24	7	19	0.9	5.6	3.4	4.4
Dickie	94	5	12	1.3	10.7	2.8	5.0
Glen	16	7	15	0.7	17.4	5.1	3.8
Gullfeather	66	5	13	1.5	11.8	2.5	5.2
Harp	71	13	38	1.7	6.7	3.8	3.9
Joseph	1737	25	80	14.0	2.9	8.4	2.0
Kimball	213	22	61	3.3	3.3	7.1	2.5
Leonard	195	7	15	1.7	5.8	5.4	3.2
Little Clear	11	8	25	0.4	6.3	5.4	2.7
Louisa	531	16	61	3.0	3.4	6.5	2.9
Maggie	129	10	31	1.8	3.8	7.1	1.5
Muskoka	2021	27	52	12.0	5.8	4.6	3.6
Pincher	42	6	16	1.1	4.8	5.0	2.3
Plastic	32	8	16	1.2	4.8	6.8	2.8
Poker	15	6	18	0.9	15.0	2.7	6.0
Poker East	5	7	21	0.4	25.0	2.6	6.3
Red Chalk	44	17	38	0.8	4.4	6.3	2.5
Rosseau	1188	23	47	7.0	4.2	6.7	2.9
Smoke	697	16	55	5.0	5.5	5.0	3.0
Solitaire	124	13	31	1.5	5.0	7.2	2.1
Timberwolf	167	7	20	2.4	7.0	3.7	4.0
Walker	68	6	17	1.1	5.8	5.3	3.4
Westward	63	21	44	0.9	3.5	7.3	1.5

values to predict oxygen concentrations at the end of the summer stratification (standardized to 1 September) for each stratum.

Oxygen concentrations at each stratum z are determined by

$$(1) \quad \log_{10}O_2(f)_z = 1.83 - 1.91/VSA_z - 7.06/O_2(i)_z - 0.0013TP_{so}^2$$

where $O_2(f)$ is the oxygen concentration at depth z at the end of summer stratification ($mg \cdot L^{-1}$), $O_2(i)$ is the oxygen concentration at depth z at spring turnover ($mg \cdot L^{-1}$), TP_{so} is the total phosphorous concentration at spring turnover ($\mu g \cdot L^{-1}$), and VSA_z is the stratum volume – interval sediment surface area ratio at stratum z (m).

Spring turnover oxygen concentrations ($O_2(i)$) are measured directly or determined for each stratum by

$$(2) \quad \log_{10}O_2(i) = 0.99 - 5.74/A_0 + 0.64/z$$

when the maximum distance from shore to shore at z_{max} (MD) < 1.4 km and A_0 is the surface area of the lake (ha), or by

$$(3) \quad \log_{10}O_2(i) = 1.07 - 6.95/A_0 - 0.0043z/MD$$

when MD > 1.4 km.

Total phosphorus was measured using an automated procedure using ascorbic acid reduction, ammonium molybdate reaction, and colorimetry. DOC was measured by an automated procedure in which samples were acidified and flushed with nitrogen to remove dissolved inorganic carbon (DIC) and then photo-oxidized to convert the DOC to DIC, which

© 2003 NRC Canada

Table 2. Location, area (A_0), mean depth ($\bar{z}$), maximum depth (z_{max}), maximum distance across lake through central basin (MD), total phosphorus (TP), Secchi depth, and dissolved organic carbon (DOC) concentration for the lakes used to test the optimal habitat model (lake set 2).

Lake	Latitude	Longitude	A_0 (ha)	$\bar{z}$ (m)	z_{max} (m)	MD (km)	TP ($\mu g \cdot L^{-1}$)	Secchi (m)	DOC (mg $C \cdot L^{-1}$)
Gull River Watershed									
Beech	45′05″	78′42″	124	7	26	2.4	8.0	5.3	3.5
Big Hawk	45′10″	78′44″	389	16	59	3.7	5.0	7.5	2.5
Boshkung	45′04″	78′44″	716	23	71	5.8	5.2	5.1	3.0
Drag	45′05″	78′24″	912	19	54	5.1	5.3	5.4	NA
Eagle	45′08″	78′31″	235	8	24	1.6	6.5	6.2	3.4
Haliburton	45′12″	78′24″	1014	18	55	3.9	5.1	5.6	3.4
Halls	45′06″	78′45″	535	28	80	3.2	3.5	8.0	2.4
Havelock	45′17″	78′38″	198	11	30	2.0	5.1	5.6	2.3
Johnson	45′16″	78′37″	151	18	44	2.0	4.3	6.5	2.5
Kabakwa	45′07″	78′48″	115	7	20	1.4	5.8	5.8	3.8
Kashagawigamog W.	44′59″	78′36″	523	15	44	5.3	7.2	4.7	4.5
Kennisis	45′13″	78′38″	1418	23	68	6.9	3.3	6.0	2.6
Kushog North	45′08″	78′49″	270	13	37	1.6	5.0	5.0	3.2
Kushog South	45′04″	78′47″	370	7	27	4.1	6.0	4.6	3.2
Lipsy	45′10″	78′38″	69	18	52	2.0	5.7	5.9	3.4
Little Hawk	45′09″	78′43″	343	27	93	4.2	4.3	8.2	2.3
Little Kennisis	45′15″	78′35″	230	15	44	2.1	5.8	4.3	3.5
Little Redstone	45′13″	78′34″	226	13	62	1.8	6.1	4.9	3.7
Margaret	45′08″	78′53″	60	11	32	1.4	4.6	8.3	2.2
Marsden	45′14″	78′31″	230	4	24	1.0	10.1	3.0	4.7
Moose	45′09″	78′28″	290	16	44	3.2	7.0	5.3	3.3
Nunikani	45′12″	78′44″	116	8	24	2.1	4.6	6.4	2.8
Oblong	45′11″	78′36″	91	10	28	1.4	7.2	4.9	3.5
Percy	45′12″	78′22″	596	11	34	2.0	6.0	4.6	4.7
Red Pine	45′12″	78′42″	365	10	39	3.4	4.4	7.8	2.6
Sherborne	45′11″	78′49″	252	10	35	1.6	5.6	5.9	2.8
Soyers	45′01″	78′37″	329	14	48	2.5	7.0	4.9	5.5
St. Nora	45′09″	50″	262	16	39	2.8	3.9	4.6	3.0
Twelve Mile	45′01″	78′43″	337	11	28	3.8	4.9	5.3	3.0
Rideau Watershed									
Big Clear	44′43″	76′28″	169	20	58	2.0	7.0	8.4	NA
Big Rideau	44′46″	76′13″	4663	15	100	10.0	19.2	4.0	NA
Big Salmon	44′32″	76′30″	172	13	42	7.0	9.0	8.0	NA
Desert	44′32″	76′35″	402	20	68	4.2	18.0	5.8	NA
Devil	44′35″	76′27″	54	14	44	2.5	15.0	5.5	NA
Loughborough	44′27″	76′25″	942	15	36	10.0	24.0	5.0	NA
Red Horse East	44′32″	76′05″	143	10	36	3.0	25.0	2.7	NA
Red Horse West	44′32″	76′05″	166	10	36	2.0	25.0	3.4	NA

Note: The data for the Gull River Watershed lakes are based on either 2- or 3-year averages, whereas the data for the Rideau Watershed lakes are averages of 1 to 6 years. NA, no data available.

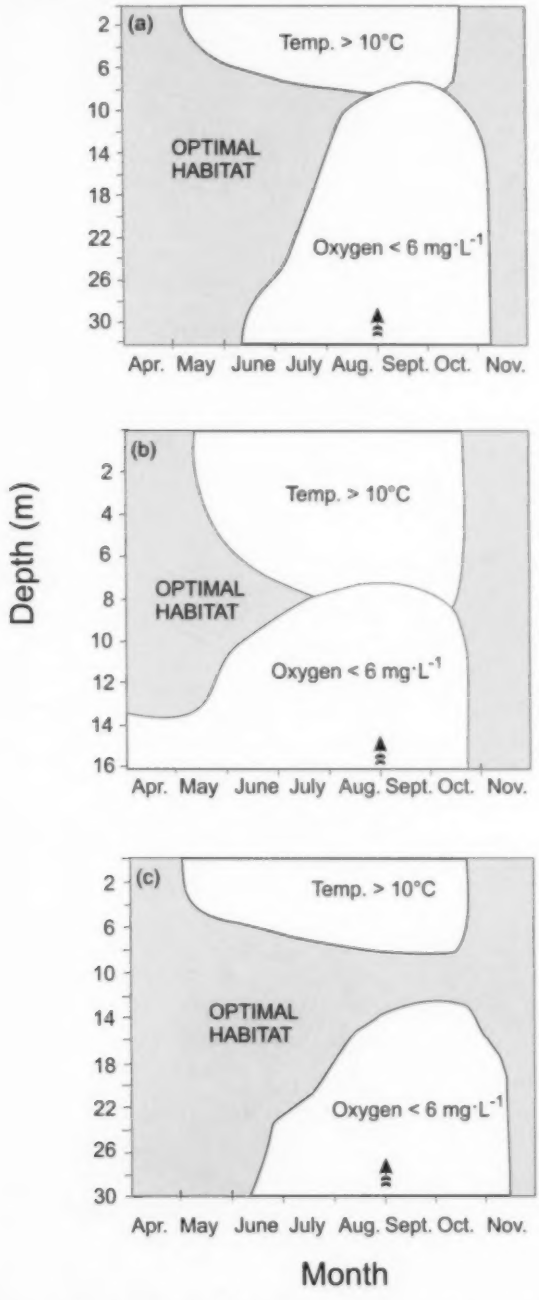
was analysed colorimetrically after reaction with a phenolphthalein solution. The analytical methods, quality assurance – quality control (QA/QC) procedures, and detection limits are described in detail in Ontario Ministry of the Environment (1983).

Study area

The oxygen model used here (Molot et al. 1992) was developed originally using data from a set of seven lakes in central Ontario that were the focus of a long-term study of the effects of nutrients, acid deposition, and trace contaminants on oligotrophic, soft-water lakes (Dillon et al. 1986) and tested subsequently on an independent set of eight lakes. An additional 17 lakes in the same region were used to test and further refine components of the model (Molot et al. 1992). More recently, the model was retested on an independent set of 42 lakes encompassing a wider range of morphometric characteristics than the original data set (Clark et al. 2002). For the development of the temperature model, the three lake sets used by Molot et al. (1992) were combined (three of the 32 lakes, Nunikani, Red Pine, and Sherborne, were excluded because they are in a watershed that was the basis for another lake set discussed below) with eight additional lakes in the same region that had adequate

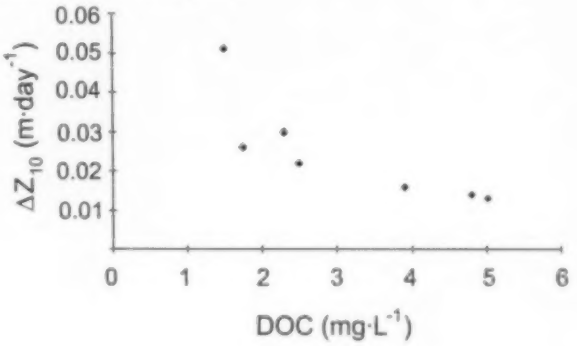
© 2003 NRC Canada

Fig. 1. Optimal habitat (shaded area) in (*a*) Harp Lake, (*b*) Walker Lake, and (*c*) Red Chalk Lake used for model development (lake set 1); the depths at which $O_2 < 6$ mg·L^{-1} and temperature (Temp.) > 10 °C are shown for one year. September 1st (marked with arrows) was chosen as the date for which optimal habitat boundaries were predicted.



data available for a total of 37 lakes (lake set 1; Table 1). Inclusion of the latter eight lakes allowed us to expand the range of lake sizes used in model development. With the exception of Glen Lake, which sits on a small dolomite deposit, all are of low ionic strength and are oligotrophic or mesotrophic. Some, such as Plastic Lake, have been affected adversely by acid deposition (Dillon et al. 1987).

Fig. 2. The relationship between the average rate that the depth of the 10 °C isotherm lowered in the water column (ΔZ_{10}) and the long-term average dissolved organic carbon (DOC) concentration in the seven lakes from lake set 1 with the longest data record (n = 16 to 19 years).



Another set of lakes was used to test the optimal habitat model developed here. Twenty-nine of the 50 lakes in the Gull River Watershed, Haliburton County, Ont., that had been utilized previously to test a nutrient model (Hutchinson et al. 1991), some of which had been used by Clark et al. (2002) to test the Molot et al. (1992) oxygen model, were identified as having well-developed hypolimnia, lake trout populations, and all of the necessary data needed to test the habitat model. An additional eight lakes with lake trout populations in the Rideau Lake drainage area in eastern Ontario, also used by Clark et al. (2002), were included in this test set (lake set 2; Table 2).

Results and discussion

Within-year differences in Z_{10} and optimal habitat

Examples of measured optimal habitats in three of the study lakes for one year (Fig. 1) indicate that lake trout habitat volumes are at their minimum each year immediately before the time when surface waters have cooled enough (to <10 °C) to be usable. This occurs before thermal destratification in the fall. At this time, oxygen concentrations in the hypolimnion will be at their minimum and the depth of the metalimnion as well as the depth of the 10 °C isotherm, Z_{10}, will be at their greatest. These dates are determined each year by the rate of cooling of the mixed layer and are therefore subject to external forces associated with weather. The oxygen model that we use describes average long-term conditions in the hypolimnion standardized to 1 September, and this date, as a result, was used to estimate Z_{10}. We have never observed lake turnover before this date. In some lakes (e.g., Red Chalk Lake; Fig. 1*c*), optimal habitat volumes continue to diminish past 1 September because Z_{10} may continue to move lower and $Z_{6\ mg\cdot L^{-1}}$ may continue (in those lakes exhibiting hypolimnetic oxygen depletion below 6 mg·L^{-1}) to rise from the bottom. It is difficult to obtain data sets that are closely spaced (temporally) to model the exact minimum

© 2003 NRC Canada

Table 3. Depth (m) of the 10 °C isotherm (Z_{10}) on 1 September for 37 lakes used in model development.

Lake	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
Basshaunt			7.2	7.3	6.2	7.3	6.5	7.4	7.4	7.1		7.4
Big Porcupine								10.3	9.3	10.0		
Bigwind	9.6	9.2	7.2	8.8	8.1	8.3	8.2		9.8	8.7	10.0	8.7
Blue Chalk	10.6	10.7	10.4	10.8	10.4	11.9	10.5	10.6	10.1	10.2	12.0	11.2
Bonnechere								8.1	7.8	8.0		
Buck	8.6	8.2	7.8	8.0	7.4		6.9		7.6	7.8	7.9	7.8
Chub	6.8	6.7	5.9	5.9	6.0	6.1	5.8	6.2	6.1	6.6	6.5	6.0
Cinder					5.8	6.1					5.6	5.4
Cinder East									6.5	5.9	5.9	5.8
Clear					11.7	11.9	11.8	12.2	12.3	11.7	12.8	12.4
Cradle											11.4	12.5
Crosson	7.9	6.9	6.7	6.7	6.1	6.4	6.1	6.8	6.6	6.5	6.3	6.5
Crown								12.2	11.7	12.2		
Crystal											9.4	9.2
Delano					6.1	6.4	6.3	6.4	6.0	6.2	6.3	5.1
Dickie	8.6	8.8	7.8	8.5	7.3	7.6	6.9	7.7	8.1	8.3	8.2	8.1
Glen			7.7	8.2	7.7	7.8	7.4	8.4	7.9	7.3	8.0	8.4
Gullfeather	8.0	9.1	6.6	6.8	6.9	7.2	6.3		8.0	7.3	7.5	7.2
Harp	8.1	7.7	7.2	7.5	6.9	7.6	7.0	7.4	7.3	7.2	7.4	7.4
Joseph											14.5	
Kimball								9.6	9.6	10.3		
Leonard					10.1	11.1			10.7	13.0	10.2	10.2
Little Clear	6.8	7.9	7.3	7.8	7.4	8.1	7.0	8.1	6.7	7.4		
Louisa						10.6	9.6		10.6	11.1		
Maggie											13.1	13.2
Muskoka											16.5	
Pincher											10.0	11.4
Plastic				9.8	9.7	10.2	10.9	12.1	10.6	11.2	11.4	10.9
Poker									5.0	4.5	4.6	4.8
Poker East					5.2	5.7			5.6	5.5	5.7	5.6
Red Chalk	8.8	8.6	8.3	8.5	7.6	8.2	8.0	8.1	8.2	8.2	8.8	8.5
Rosseau											12.8	
Smoke						10.7	10.0	10.5	10.2	12.1		
Solitaire	11.8	12.4	11.2	11.1	10.6	11.2	9.6	12.2	10.5	10.0		11.6
Timberwolf							8.5	9.1	8.8	9.8		
Walker	9.6	9.1	8.7	8.9	8.0	9.0	8.2	9.2	8.8	8.2		8.7
Westward						13.5	10.6	11.9	10.7	11.1	10.0	11.6

Note: The number of years with data varies between 3 and 19. Standard deviation (SD) and coefficient of variation (CV) are reported.

habitat volumes or to predict the dates that these occur as a result of the between-year variation in the turnover dates. By the end of September, however, temperatures are almost always such that optimal habitat for lake trout (Evans et al. 1991) has started to increase.

We examined the rate of depression of Z_{10} during the summer and fall period for the seven lakes with the longest data records. These rates ranged from 0.013 to 0.051 m·day^{-1} and were correlated with transparency (as DOC) for this set of lakes (Fig. 2). This suggests that Z_{10} would not likely depress by more than ~1.5 m after 1 September, even if conditions continue to deteriorate for the entire month. Oxygen concentrations in the bottom waters may continue to diminish, and this would potentially present more severe problems for lake trout, especially in those cases in which habitat volumes are minimal earlier in the year, a situation usually found in lakes that are relatively shallow (Sellers et al. 1998). The greatest stress on populations occurs after all of the optimal habitat has disappeared. Hence, we believe that the optimal habitat estimated for 1 September describes close to minimal volumes.

Between-year differences in Z_{10}

Measured Z_{10}s for the 37 model development lakes (lake set 1) for all years with available data suggest that between-year variation in measured Z_{10}s for a given lake was much smaller than the observed variation in the long-term mean among lakes (Table 3). Mean long-term Z_{10}s ranged almost threefold, from 4.8 to 14.5 m, over the range of lakes used in the study, whereas the standard deviations for each lake ranged from 0.1 to 1.8 m (mean coefficient of variation 7%) with only six of the 37 lakes having standard deviations of 1 m or more. Although there was some indication that the year-to-year variation in the observed Z_{10}s was greater in

© 2003 NRC Canada

1988	1989	1990	1991	1992	1993	1994	*n*	Mean	SD	CV
7.7		7.4	7.3				12	7.2	0.4	5.6
							3	9.9	0.5	5.0
	9.4		8.4				13	8.8	0.8	9.1
10.8	10.8	10.9	10.3	10.4	10.5	10.9	19	10.7	0.5	4.7
							3	8.0	0.1	1.9
8.6			7.6				12	7.8	0.5	6.4
6.3	5.7	6.5	5.9	5.6	5.6	5.8	19	6.1	0.4	6.6
5.9	5.2	5.4	5.3				8	5.6	0.3	5.4
6.1	5.1	5.7	5.5				8	5.8	0.4	6.9
12.5	11.6	12.7	11.0				12	12.0	0.5	4.2
12.0	10.5	11.4	11.8				6	11.6	0.7	6.0
6.7	6.1	6.1	6.5	6.4	5.9	5.9	19	6.5	0.5	7.7
							3	12.0	0.3	2.5
9.6	8.8	9.1	8.3	8.3			7	9.0	0.5	5.6
5.9	5.9	5.6					11	6.0	0.4	6.7
7.7	6.7	7.5	7.1	6.4	7.3	7.9	19	7.7	0.7	9.1
8.3	8.6	8.6					13	8.0	0.4	5.0
6.9		7.2					13	7.3	0.7	9.6
7.5	6.9	7.6	7.3	7.1	6.7	7.1	19	7.3	0.3	4.1
		13.4	11.5	12.7	14.5		5	13.3	1.3	9.8
							3	9.8	0.4	4.1
10.6	9.0	9.7	8.6				10	10.3	1.2	11.7
8.4			7.7				12	7.5	0.5	6.7
							4	10.5	0.6	5.7
13.7	13.0	14.5	13.5	12.3			7	13.3	0.7	5.3
		13.5	12.0	13.5	16.5	15.0	6	14.5	1.8	12.4
11.1	8.5	8.6	9.3	7.5	7.9		8	9.3	1.4	15.1
12.1	10.7	11.9	11.4	10.8	9.6	10.9	16	10.9	0.8	7.3
5.1	4.7	4.6	4.9	4.9			9	4.8	0.2	4.2
6.0		5.1	5.4	5.6			10	5.5	0.3	3.6
8.7	8.8	8.1	8.4	7.7	7.5	7.4	19	8.2	0.4	4.9
		11.5	9.8	11.7	12.5		5	11.8	1.2	10.2
							5	10.7	0.8	7.5
10.9			10.8				13	11.1	0.8	7.2
							4	9.1	0.6	6.6
8.8	8.7	9.1	8.8				15	8.8	0.4	4.5
10.0	9.2	11.6	11.4	10.4	10.9	10.6	14	11.0	1.0	9.1

lakes with greater transparency as measured by DOC, the relationships between the standard deviation of Z_{10} and neither the average concentration of DOC ($r = 0.30$, $p = 0.07$) nor the average Secchi depth ($r = 0.23$, $p = 0.18$) were significant. It is worth noting that the one extremely large lake in lake set 2 (Big Rideau Lake; Tables 2 and 4) showed a very high degree of between-year variation in the measured Z_{10}, with values varying between 12 and 20 m.

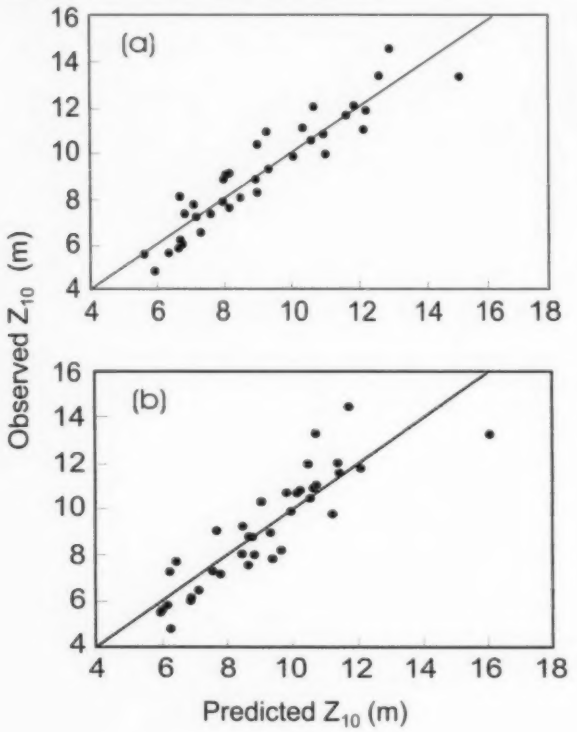
The measured between-year variation in Z_{10} was investigated in the seven lakes (Blue Chalk, Chub, Crosson, Dickie, Harp, Plastic, and Red Chalk) with the longest data records (Table 3). Even though the coefficient of variation in Z_{10} in these seven lakes averaged only 6% and the between-year differences in DOC were not great, in four of the seven lakes (with range in DOC between years of ca. 1.0–1.2 mg C·L^{-1} in each of the four lakes), Z_{10} was negatively correlated ($p < 0.05$) with annual DOC concentration. Two of the three lakes that had no such correlation had almost no variability in DOC (<0.5 mg C·L^{-1}) over the 16–19 years.

Z_{10} model

In each of the lakes, the 10 °C isotherm generally was found within the metalimnion at 1 September. On the basis of previously published studies, we suspected that this depth would be determined by a combination of lake size expressed as area or fetch and by transparency. For example, Fee et al. (1996) found that for the wide range of lake sizes in his study (3 – 30 000 ha), lake area (A_0) was the primary determinant of the depth of the mixed layer (the epilimnion) in summer. The relationship was modified significantly by transparency for lakes less than 500 ha. Similarly, Gorham and Boyce (1989) related the depth of the summer thermocline to $\sqrt{A_0}$ for lakes with a cross-basin diameter less than 5 km, and Mazumder and Taylor (1994) related mid-summer

© 2003 NRC Canada

Fig. 3. Observed vs. predicted depths (m) of the 10 °C isotherm (Z_{10}) in lake set 1 based on models using (*a*) dissolved organic carbon (eq. 4) and (*b*) Secchi depth (eq. 5).



epilimnion depth to lake size and water clarity in a large set of lakes in Ontario. More recently, Perez-Fuentetaja et al. (1999) reported that average thermocline depth in small Precambrian lakes in Ontario was controlled by DOC, with lake area and mean depth as secondary influences. Similarly, Snucins and Gunn (2000) found that water clarity and lake depth strongly influenced the thermal structure of small lakes (2–404 ha) located in Killarney Park near Sudbury, Ont.

To develop the temperature boundary model, we used long-term, average values from lake set 1 for Secchi depth and DOC concentration during the ice-free period, together with maximum depth (z_{max}), lake area (A_0), and maximum distance measured through the deepest location (MD) as independent variables in the model (Table 1). We also used total phosphorus (TP) as an independent variable as it is very strongly correlated with chlorophyll *a* concentration (Dillon and Rigler 1974; Molot and Dillon 1991), another parameter that affects water clarity.

For the set of 37 lakes used for model development, transparency was the primary determinant of Z_{10}, with the morphometric or lake size parameters playing a secondary role. Either water clarity parameter, Secchi depth or 1/DOC (we used the reciprocal of the dissolved organic carbon concentration to generate a linear relationship), together with either lake area or MD gave the strongest relationships. The combination of 1/DOC and A_0 (Fig. 3*a*) gave the best fit:

Table 4. Comparison between predicted (Pred.) and observed (Obs.) depths (m) of 10 °C and 6 mg $O_2 \cdot L^{-1}$ for the set of lakes used for model testing (lake set 2).

		Z_{10} (m)		$Z_{6\ mg \cdot L^{-1}}$	
Lake	*n*	Pred.	Obs.	Pred.	Obs.
Gull River Watershed					
Beech	2	9	11	10	12
Big Hawk	1	12	10	49	47
Boshkung	2	10	11	47	50
Drag	10	10	10	42	52
Eagle	2	10	10	10	10
Haliburton	2	10	9	43	48
Halls	2	12	11	76	76
Havelock	2	9	11	20	19
Johnson	2	10	11	36	32
Kabakwa	1	9	10	9	10
Kashagawigamog W.	1	10	8	39	42
Kennisis	2	11	12	64	72
Kushog North	2	9	9	33	36
Kushog South	2	9	10	17	10
Lipsy	2	10	10	29	37
Little Hawk	1	13	12	79	80
Little Kennisis	1	8	8	39	41
Little Redstone	2	9	9	51	49
Margaret	1	12	12	17	17
Marsden	2	7	8	8	7
Moose	2	10	9	32	33
Nunikani	4	10	10	14	13
Oblong	2	9	8	14	14
Percy	2	8	10	22	22
Red Pine	2	12	12	29	32
Sherborne	3	10	10	25	17
Soyers	1	9	8	44	47
St. Nora	3	9	9	36	34
Twelve Mile	12	10	10	19	15
Rideau Watershed					
Big Clear	5	12	12	47	48
Big Rideau	6	9	16	80	87
Big Salmon	4	13	12	29	27
Desert	1	10	10	58	63
Devil	3	9	11	Z_{ox}	14
Loughborough	1	12	14	12	19
Red Horse East	1	8	10	Z_{ox}	7
Red Horse West	1	7	9	Z_{ox}	7

Note: Z_{ox} indicates that there is no depth in the hypolimnionn at which there is 6 mg $O_2 \cdot L^{-1}$.

$$(4) \quad Z_{10} = 3.52 + 11.3/\mathrm{DOC} + 0.139\sqrt{A_0}$$

($r^2 = 0.88$, $p < 0.000001$, standard error of estimate = 0.87)

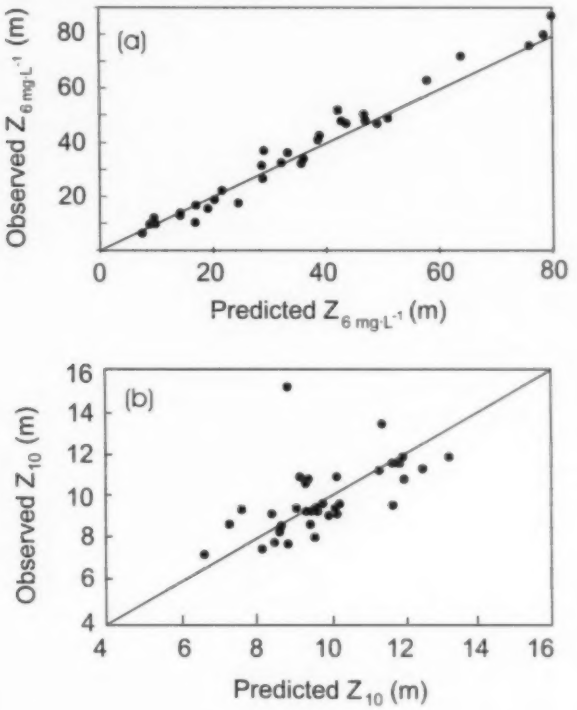
which was somewhat better than the fit obtained using Secchi depth as the transparency parameter (Fig. 3*b*):

$$(5) \quad Z_{10} = 3.35 + 0.956\mathrm{Secchi} + 0.33\mathrm{MD}$$

($r^2 = 0.78$, $p < 0.000001$, standard error of estimate = 1.17)

© 2003 NRC Canada

Fig. 4. Observed vs. predicted depths (m) of the optimal habitat boundaries in the lakes (lake set 2) used to test the models: (*a*) the $Z_{6\ mg\cdot L^{-1}}$ boundary based on eq. 1 and (*b*) the Z_{10} boundary based on eq. 5. The lines shown are the 1:1 lines.



However, because Secchi depth data are generally more often available and are easier to collect and because the oxygen model requires MD as an input, eq. 5 may be potentially more useful. In the subsequent tests with independent data, we have used both of the models.

Prediction of optimal habitat

To test the temperature (Z_{10}) and oxygen ($Z_{6\ mg\cdot L^{-1}}$) models' ability to define the upper and lower boundaries of the optimal habitat, a second data set was used (Table 2). The predicted $Z_{6\ mg\cdot L^{-1}}$ values (eq. 1) and Z_{10} values (eq. 5) were then compared with the observed data (Table 4; Fig. 4). Although for both models the slope of the line of predicted vs. observed Z_{10} and $Z_{6\ mg\cdot L^{-1}}$ values is not significantly different from 1 ($p < 0.01$), the fit between observed and predicted results appears to be better for the $Z_{6\ mg\cdot L^{-1}}$ model (Fig. 4*a*; $r^2 = 0.97$, $p < 10^{-6}$) than for the Z_{10} model (Fig. 4*b*; $r^2 = 0.35$, $p < 0.0002$). This is largely a result of the much greater range of depths in the former than in the latter. Whereas the observed Z_{10} in lake set 2 varies by a factor of 2 (between 7.8 and 15.7 m), $Z_{6\ mg\cdot L^{-1}}$ varies more than 12-fold, from 7 to 87 m. In fact, the standard error of the predicted Z_{10} is substantially less (1.4 m) than that of the predicted $Z_{6\ mg\cdot L^{-1}}$ (3.6 m). Secondly, the comparisons of the predictions and observations using the Z_{10} model (Fig. 4*b*) are affected greatly by a single lake, Big Rideau. This lake has an A_0 of 4663 ha, which is well beyond the range of lake sizes (i.e., 5–2021 ha) used to develop the model (Table 1); the results therefore indicate that caution should be exercised when extrapolating the Z_{10} model to very large lakes. When Big Rideau Lake is removed from the comparison, the r^2 increases from 0.35 to 0.60 and the standard error drops to 0.9 m.

We also compared predicted and measured Z_{10}s based on eq. 4 using DOC and A_0 instead of eq. 5 (using Secchi and MD). The relationship between the observed and predicted values was as good ($r^2 = 0.36$, $p < 0.001$) as that obtained using eq. 5 with Big Rideau Lake included but was poorer than the relationship using Secchi and MD with Big Rideau excluded. However, because there were no DOC data available for some of the lakes in lake set 2, including all of those in the Rideau Watershed, it was not possible to determine whether the DOC–A_0 version of the Z_{10} model was as good as the Secchi–MD version. For this reason and because of the widespread availability of Secchi depth data, we have chosen to use eq. 5 rather than eq. 4 for predicting the optimal habitat volumes below.

The predicted and observed absolute optimal habitat (OH) volumes, expressed as both absolute volumes and as a percent of the total volume of the lakes (Table 5), were in very close agreement ($r^2 = 0.996$, $p < 10^{-6}$), but this is due partly to the great range in size of the different lakes. A more useful test of the model is obtained by comparing predicted and observed proportional volumes (percent of the total lake volume that is optimal habitat). The comparison was again excellent (Table 5; $r^2 = 0.98$, $p < 10^{-6}$) and indicates that the two models together can be used to make accurate predictions of lake trout habitat.

Although the predictions of both proportional and absolute lake trout OH volume compared very favorably with the measured amounts, some of the variation between predicted and observed volumes must result from comparing predicted volumes based on a model developed using long-term, average conditions with observed results based, in most cases, on a very few, usually two, years of data. When examining the between-year variability in OH volume for Twelve Mile Lake, the lake in lake set 2 with the longest period of record (12 years), it is clear that considerable variation in habitat volume occurred among years, primarily as a result of variability in $Z_{6\ mg\cdot L^{-1}}$ (Fig. 5). Thus estimates of OH volume based on 1 or 2 years of data may be imprecise. Other factors or parameters that were not included in either of the models defining the habitat boundaries may be important. For example, France (1997) established linkages between lake thermocline depth and riparian deforestation, which would indicate that the Z_{10} for lakes of similar size, clarity, and nutrient status might vary with differences in riparian cover or surrounding topography. We cannot quantify the influence of this parameter on the variation observed between predicted and measured boundary depths as such data are not available.

Effects of external stresses on habitat volume

Because the two components of the OH model, the oxygen boundary model and the temperature boundary model, use only TP, Secchi depth (or DOC), and physical factors (morphometry, MD), changes in either the nutrient status or transparency of a lake will impact directly the optimal habitat volumes. These relationships, in fact, allow us to predict

© 2003 NRC Canada

Table 5. Comparison between predicted (Pred.) and observed (Obs.) optimal habitat (OH) expressed as absolute volumes (10^4 m^3) and as relative proportion (%) of the total volume for the test set of lakes.

	OH (absolute)		OH (relative)	
Lake	Pred.	Obs.	Pred.	Obs.
Beech	0	16	0	2
Big Hawk	2 940	3 280	48	53
Boshkung	10 500	10 400	63	62
Drag	10 200	11 200	55	59
Eagle	0	0	0	0
Haliburton	9 800	9 110	54	51
Halls	9 350	9 820	62	65
Havelock	609	463	29	22
Johnson	1 390	1 220	52	45
Kabakwa	0	0	0	0
Kashagawigamog W.	4 120	4 530	51	56
Kennisis	19 300	19 100	59	59
Kushog North	1 570	1 590	46	47
Kushog South	460	44	18	2
Lipsy	550	637	45	51
Little Hawk	5 930	6 170	63	66
Little Kennisis	1 800	1 860	53	55
Little Redstone	1 430	1 390	50	49
Margaret	107	95	16	14
Marsden	0	0	0	0
Moose	2 260	2 360	50	52
Nunikani	120	107	14	12
Oblong	222	225	24	25
Percy	1 520	1 360	39	35
Red Pine	1 040	1 070	28	29
Sherborne	760	550	32	23
Soyers	2 490	2 680	54	58
St. Nora	2 290	2 200	56	54
Twelve Mile	1 010	815	28	23
Big Clear	1 760	1 790	48	49
Big Rideau	41 600	32 800	55	43
Big Salmon	810	830	33	34
Desert	4 950	5 140	58	60
Devil	0	85	0	7
Loughborough	0	0	0	0
Red Horse East	0	0	0	0
Red Horse West	0	0	0	0

the loss in OH volume that would result from projected changes in water quality. It should be noted that in some instances, the changes in conditions controlling Z_{10} and $Z_{6\ mg\cdot L^{-1}}$ may, in part, have counteracting effects on OH volume. Increasing nutrient levels (TP), for example, will increase oxygen deficits near the bottom (Molot et al. 1992), resulting in a shallower lower boundary for optimal habitat. However, the same change in TP may result in reduced Secchi depth because of increased chlorophyll *a* concentrations (Dillon and Rigler 1974), a shallower Z_{10}, and therefore increased habitat volume. In general, however, water clarity in lake trout lakes is controlled by DOC rather than by TP, so the effects of an increase in nutrient levels will be largely transmitted through the decrease in the lower oxygen

Fig. 5. Variation in measured optimal habitat (OH; darker shaded area) boundaries in Twelve Mile Lake from 1981 and 1995 showing most of the variability in the lower ($Z_{6\ mg\cdot L^{-1}}$) boundary. Diamonds represent Z_{10} and squares represent $Z_{6\ mg\cdot L^{-1}}$.

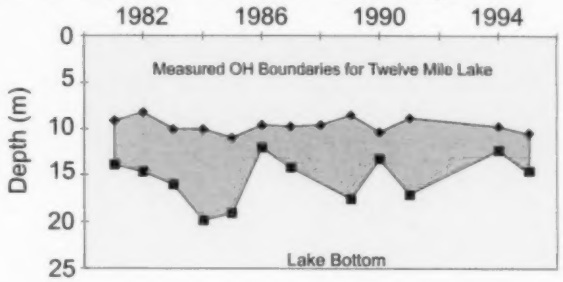
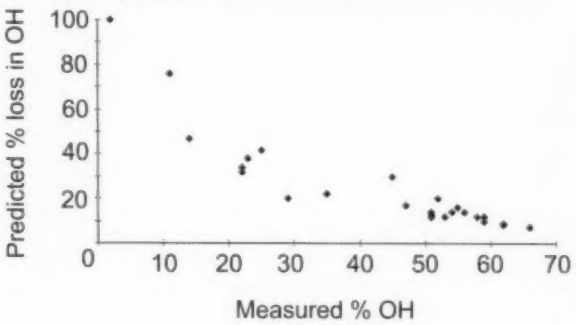


Fig. 6. Relationship between the predicted proportion (%) of the optimal habitat (OH) that will be lost if Secchi depth increases by 2 m in the lakes in lake set 2 and the measured optimal habitat volume expressed as a percent of the whole-lake volume.



boundary rather than the increase in the upper temperature boundary.

Many lakes will likely become more transparent as a consequence of changes in climate (Magnuson et al. 1997; Schindler et al. 1996*a*, 1997). It has been proposed that this will be the result of declining DOC production in watersheds during prolonged periods of above-normal temperature and below-normal precipitation (Dillon et al. 1996; Dillon and Molot 1997; Schindler et al. 1997). This increase in transparency in combination with the direct effects of increased air temperatures will result in deeper Z_{10}s (Snucins and Gunn 2000) and decreased optimal lake trout habitat volumes. Fee et al. (1996) estimated that there is the potential for the epilimnia in smaller lakes to increase in thickness by 1–2 m as the result of a twofold increase in atmospheric CO_2 levels. Acidification of lakes by the input of mineral acids also results in increased transparency (Effler et al. 1985), again via removal of DOC (Schindler et al. 1996*b*). For example, the Secchi depth measured in Plastic Lake increased by ~2 m (Dillon et al. 1987) during the lake's last 7 or 8 years of acidification and probably by much more over the total period in which acidification occurred. For the lakes in our study, each 1 m increase in transparency would result in a predicted increase in Z_{10} of ~1 m. Following a 2-m increase in transparency, OH volumes in the 37 lakes used to test the model would be reduced by between 8% and 100% (eq. 5 and Fig. 6). These calculations are based on the assumption

© 2003 NRC Canada

that clarity changes result from loss of DOC and that there is no change in TP concentrations affecting the lower OH boundaries ($Z_{6\ mg \cdot L^{-1}}$). Any such changes resulting from changes in TP would be much less significant than those resulting from DOC-induced changes in clarity. The proportional amount of OH that would be lost for any lake is greatest when the OH volume is relatively small. Lakes having high percentages (>50%) of their total volume as optimal habitat would lose only 10–20% of their optimal habitat, whereas lakes with only 10–25% of their volume as optimal habitat could lose 50% or more of the remaining habitat, putting the continued success of the lake trout populations in jeopardy.

In summary, simple models requiring only limited limnological information (morphometry, TP concentration, and Secchi depth or DOC concentration) can be used to estimate the depth of the upper (temperature-controlled) and lower (oxygen-controlled) boundaries defining optimal habitat for lake trout. These boundaries are based on temperature (10 °C) and oxygen (6 $mg \cdot L^{-1}$) criteria reported in the literature; an analogous approach can be used to estimate the location of any other habitat boundaries (e.g., usable habitat) defined in terms of temperature and oxygen. The upper and lower habitat boundary models were developed and then tested on independent sets of study lakes. Predicted and measured optimal habitat volumes in the test set of lakes were in excellent agreement. The effects of a 2-m increase in average Secchi depth, an increase that is expected to occur in many lakes if current climate change effects scenarios are accurate and one that may, in many cases, underestimate the effect of lake acidification, were evaluated. Under this scenario, lakes with a relatively small portion (<25%) of their total volume suitable for lake trout may lose most of the available optimal habitat.

Acknowledgements

Many people have helped to collect these long-term data sets. In particular, we thank Joe Findeis, Bob Girard, and Ron Reid.

References

Christie, G.C., and Regier, H.A. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. **45**: 301–314.

Clark, B.J. 1996. Limnological sample and data collection methods used by the Muskoka Lakes Aquatic Assessment Unit. Ont. Min. Environ. Energy Tech. Rep. ISBN 0-7778-5757-X.

Clark, B.J., Dillon, P.J., Molot, L.A., and Evans, H.E. 2002. Application of a hypolimnetic oxygen profile model to lakes in Ontario. Lake Reservoir Manag. **18**: 32–43.

Dillon, P.J., and Molot, L.A. 1997. Effect of landscape form on export of dissolved organic carbon, iron and phosphorus from forested stream catchments. Water Resour. Res. **33**: 2591–2600.

Dillon, P.J., and Rigler, F.H. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. **19**: 767–773.

Dillon, P.J., Nicholls, K.H., Scheider, W.A., Yan, N.D., and Jeffries, D.S. 1986. Lakeshore capacity study, trophic status. Research and Special Projects Branch, Ontario Ministry of Municipal Affairs and Housing, Toronto, Ont. ISBN 0-7743-8077-2.

Dillon, P.J., Reid, R.A., and deGrosbois, E. 1987. The rate of acidification of aquatic ecosystems in Ontario, Canada. Nature (Lond.), **329**: 45–48.

Dillon, P.J., Molot, L.A., and Futter, M. 1996. The effect of El Nino-related drought on the recovery of acidified lakes. Environ. Monit. Assess. **46**: 105–111.

Effler, S.W., Schafran, G.C., and Driscoll, C.T. 1985. Partitioning light attenuation in an acidic lake. Can. J. Fish. Aquat. Sci. **42**: 1707–1711.

Evans, D.O., and Olver, C.H. 1995. Introduction of lake trout (*Salvelinus namaycush*) to inland lakes of Ontario, Canada: factors contributing to successful colonization. J. Great Lakes Res. **21**(Suppl. 1): 30–35.

Evans, D.O., Casselman, J.M., and Willox, C.C. 1991. Effects of exploitation, loss of nursery habitat, and stocking on the dynamics and productivity of lake trout populations on Ontario lakes. Lake trout synthesis, Response to Stress Working Group. Ont. Min. Nat. Resour., Toronto, Ont.

Fee, E.J., Hecky, R.E., Kasian, S.E.M., and Cruikshank, D.R. 1996. Effects of lake size, water clarity, and climate variability on mixing depths in Canadian Shield Lakes. Limnol. Oceanogr. **41**: 912–920.

France, R. 1997. Land–water linkages: influences of riparian deforestation on lake thermocline depth and possible consequences for cold stenotherms. Can. J. Fish. Aquat. Sci. **54**: 1299–1305.

Gorham, E., and Boyce, F.M. 1989. Influence of lake surface area and depth on thermal stratification and the depth of the summer thermocline. J. Great Lakes Res. **15**: 233–245.

Girard, R., and Reid, R.A. 1990. Dorset Research Centre study lakes: sampling methodology (1986–1989) and lake morphometry. Ont. Min. Environ. Data Rep. DR 90/4. ISBN 0-7729-7021-1.

Hutchinson, N.J., Neary, B.P., and Dillon, P.J. 1991. Validation and use of Ontario's trophic status model in establishing development guidelines. Lake Reservoir Manag. **7**: 13–23.

Magnuson, J.J., Webster, K.E., Assel, R.A., Bowser, C.J., Dillon, P.J., Eaton, J.G., Evans, H.E., Fee, E.J., Hall, R.I., Mortsch, L.R., Schindler, D.W., and Quinn, F.H. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield region. Hydrol. Process. **11**: 828–871.

Martin, N.V., and Olver, C.H. 1980. The lake charr, *Salvelinus namaycush*. *In* Charrs: salmonid fishes of the genus *Salvelinus*. Perspectives in vertebrate science. Vol. 1. *Edited by* E.K. Balon. Dr. W. Junk (Publ), The Hague. pp. 209–277.

Mazumder, A., and Taylor, W.D. 1994. Thermal structure of lakes varying in size and water clarity. Limnol. Oceanogr. **39**: 968–976.

Molot, L.A., and Dillon, P.J. 1991. Nitrogen–phosphorus ratios and the prediction of chlorophyll in phosphorus-limited lakes in central Ontario. Can. J. Fish. Aquat. Sci. **48**: 140–145.

Molot, L.A., and Dillon, P.J. 1997. Photolytic regulation of dissolved organic carbon in northern lakes. Global Biogeochem. Cycles, **11**: 357–365.

Molot, L.A., Dillon, P.J., Clark, B.J., and Neary, B.P. 1992. Predicting end-of-summer oxygen profiles in stratified lakes. Can. J. Fish. Aquat. Sci. **49**: 2363–2372.

Ontario Ministry of the Environment. 1983. Handbook of analytical methods for environmental samples. Vols. 1 and 2. Ontario Ministry of the Environment, Toronto, Ont.

Ontario Ministry of the Environment and Ontario Ministry of Natural Resources. 1986. Inland lake trout management in eastern Ontario. Ont. Min. Environ. and Ont. Min. Nat. Resour. Ms. Rep.

Ontario Ministry of the Environment and Ontario Ministry of Natural Resources. 1993. Inland lake trout management in southeastern Ontario. Ont. Min. Environ. and Ont. Min. Nat. Resour. Ms. Rep.

© 2003 NRC Canada

Perez-Fuentetaja, A., Dillon, P.J., Yan, N.D., and McQueen, D.J. 1999. Significance of dissolved organic carbon in the prediction of thermocline depth in small Canadian shield lakes. Aquat. Ecol. **33**: 127–133.

Ryan, P.A., and Marshall, T.R. 1994. A niche definition for lake trout (*Salvelinus namaycush*) and its use to identify populations at risk. Can J. Fish. Aquat. Sci. **51**: 2513–2519.

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. Hydrol. Process. **11**: 1043–1067.

Schindler, D.W., Bayley, S.E., Parker, S.E., Beaty, K.G., Cruikshank, D.R., Fee, E.J., Schindler, E.U., and Stainton, M.P. 1996*a*. The effects of climate warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. Limnol. Oceanogr. **41**: 1004–1017.

Schindler, D.W., Curtis, P.J., Parker, B.R., and Stainton, M.P. 1996*b*. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. Nature (Lond.), **379**: 705–708.

Schindler, D.W., Curtis, P.J., Bayley, S.E., Parker, B.R., Beaty, K.G., and Stainton, M.P. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. Biogeochemistry (Dordr.), **36**: 9–28.

Selgeby, J.H., Eshenroder, R.L., Kreuger, C.C., Marsden, J.E., and Pycha, R.L. (*Editors*). 1995. International Conference on Restoration of Lake Trout in the Laurentian Great Lakes. J. Great Lakes Res. **21**(Suppl. 1).

Sellers, T.J., Parker, B.R., Schindler, D.W., and Tonn, W.M. 1998. Pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light. Can. J. Fish. Aquat. Sci. **44**: 170–179.

Snucins, E.J., and Gunn, J. 1995. Coping with a warm environment: behavioral thermoregulation by lake trout. Trans. Am. Fish. Soc. **124**: 118–123.

Snucins, E.J., and Gunn, J. 2000. Interannual variation in the thermal structure of clear and colored lakes. Limnol. Oceanogr. **45**: 1639–1646.

© 2003 NRC Canada

Differential response of marine populations to climate forcing

Kevin S. McCann, Louis W. Botsford, and Alan Hasting

Abstract: In searching for causes of fluctuations in marine populations, investigators often assume that populations respond on the same time scale as the environmental forcing period, but this may not hold true. Here we show how the response of populations to variable recruitment changes with the degree of overcompensation using models of two species with similar age structure but different density-dependent recruitment, chinook salmon (*Oncorhynchus tshawytscha*) and Dungeness crab (*Cancer magister*). For compensatory density dependence, as in chinook salmon, variability in recruitment tends to follow the period in environmental variability over all time scales. For overcompensatory density dependence, as in Dungeness crab, variability in recruitment follows the environmental variability only for periods much greater than the maximum age of the population. For periods in environmental variability less than the maximum age, the dominant period of the population response is slightly larger than the length of the age structure. Here, strong overcompensatory recruitment acts to filter out potentially good recruitment years, resulting in dominant periodicities slightly larger than the length of the age structure. These mechanisms appear to explain the differences between observed spectra of Dungeness crab and chinook salmon.

Résumé : Dans leurs recherches sur les causes des fluctuations des populations marines, les chercheurs assument souvent que les populations réagissent à la même échelle temporelle que la période de forçage de l'environnement, ce qui n'est peut-être pas le cas. Nous démontrons comment les réactions de populations à un recrutement variable changent en fonction du degré de surcompensation à l'aide de modèles de deux espèces qui ont des structures en âges semblables, mais des recrutements dépendant de la densité différents, le saumon quinnat (*Oncorhynchus tshawytscha*) et le crabe dormeur (*Cancer magister*). Dans un cas de densité dépendance compensatoire, comme chez le saumon quinnat, la variabilité du recrutement tend à suivre la périodicité de la variabilité environnementale sur toutes les échelles temporelles. Dans un cas de densité dépendance surcompensatoire, comme chez le crabe dormeur, la variabilité du recrutement suit la variabilité de l'environnement seulement pour les périodes qui dépassent de beaucoup l'âge maximal de la population. Pour les périodicités de variabilité environnementale inférieures à l'âge maximal, la période dominante de réaction de la population est un peu plus longue que la longueur de la structure en âges. Dans ce cas, le fort recrutement surcompensatoire sert à éliminer les années potentielles de bon recrutement, ce qui produit des périodicités dominantes un peu plus longues que la longueur de la structure en âges. Ces mécanismes semblent expliquer les différences dans les spectres observés chez le crabe dormeur et le saumon quinnat.

[Traduit par la Rédaction]

Introduction

Although marine ecologists have recognized the importance of interactions between abiotic and biotic processes for some time now (e.g., Steele and Henderson 1984; Collie and Spencer 1994), gaining an understanding of this coupling is not trivial. Researchers have empirically demonstrated that climatic variability influences marine populations and communities; however, the dynamic consequences of those effects are still largely not well understood (e.g., Pearcy 1997; McGowan et al. 1998). Much effort has been invested in searching for correlations between records of biological variables (e.g., catch) and variables reflecting the physical environment, (e.g., ocean temperature, upwelling index) at interannual (Botsford et al. 1989; Pearcy 1997) and decadal time scales (Hollowed and Wooster 1992; Francis et al. 1998). Although these approaches have proven insightful, investigators have seldom considered whether we should expect all species to track climatic variability (although see Nisbet and Gurney (1976)). Can we expect all populations to passively follow observed environmental variability — the tacit assumption in linear correlation analysis — or will some populations interact with physical processes in more complicated ways? Can we expect the time scales of vari-

Received 9 September 2002. Accepted 27 May 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 25 September 2003.
J17087

K.S. McCann.[1,2] Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, QC H3A 1B1, Canada.
L.W. Botsford. Department of Fisheries and Wildlife, University of California, Davis, CA 95616, U.S.A.
A. Hastings. Department of Environmental Sciences and Policy, University of California, Davis, CA 95616, U.S.A.

[1]Corresponding author (e-mail: ksmccann@uoguelph.ca).
[2]Present address: Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada.

 doi: 10.1139/F03-078 © 2003 NRC Canada

ability in population abundance or recruitment to be the same as the time scales of environmental forcing variables? If not, how are they related? This knowledge would prove of significant help in interpreting and predicting the long-term effects of climate change on populations and in structuring management decisions for exploited marine populations.

Here we address the general question of how different populations can be expected to respond to environmental forcing using marine populations as examples. This question is of considerable interest for many exploited marine populations, especially coastal populations in the northeastern Pacific Ocean, which are subject to ocean variability on interannual to decadal time scales. To illustrate differences in response to environmental forcing, we focus on two species influenced by the California Current that have important differences in life history: the Dungeness crab (*Cancer magister*) and Pacific salmon (e.g., chinook (*Oncorhynchus tshawytscha*)). These taxa are used to highlight a general point: that the responses of populations to abiotic forces are determined, in part, by the nature of the endogenous density-dependent biotic processes of the population. Here, we show that the model view of the natural world as a set of linear processes that responds directly to a variable environment overlooks the crucial implications of the coupling of temporal variability and density-dependent processes (e.g., Myers et al. 1998; Bjornstad and Grenfell 2001).

In what follows, we first discuss the life history of Dungeness crab and chinook salmon before discussing the important physical processes that are influencing marine populations of the California Current system. We then introduce some age-structured models that allow us to explore the implications of environmental forcing on these sets of different life history strategies (i.e., Dungeness crab and Pacific salmon).

Fisheries of the Northeast Pacific: Dungeness crab and chinook salmon as case examples

The Dungeness crab lives its entire life in the ocean environment. Females mate in spring, extrude eggs in early fall, and release larvae into the plankton near the beginning of the calendar year. The planktonic larval stage is ~4 months in duration, with metamorphosis and settlement to the near shore occurring in late spring. Adults enter the male-only fishery primarily at age 4 (Wainwright and Armstrong 1993), and fishing intensity is so high that the long-term catch record can be considered to be a reliable proxy for the number of adult males, which, in turn, will be proportional to recruitment 4 years earlier, assuming no density dependence in survivorship after recruitment. A cycle of ~10 years is apparent in these data, and it is relatively synchronous along the coast (Botsford et al. 1989; Botsford and Hobbs 1995). Considerable effort has focused on determining the roles that both internal density dependence and the exogenous environment play in the generation of these cycles.

Analyses of density dependence as a cause of these cycles involved determining how life history characteristics affected the stability of equilibria in these models and the characteristics of consequent limit cycles (Botsford and Wickham 1978; McKelvey et al. 1980). Results from these analyses indicated (*i*) that cycles are more likely when the (negative) slope of recruitment versus adult abundance is steeper and when the adult age structure is narrower, with higher mean age, and (*ii*) that the period of the limit cycles is about twice the mean age of adults. Possible mechanisms of density-dependent recruitment include cannibalism on newly settled individuals (Gotshall 1977; Botsford and Hobbs 1995), density-dependent fecundity (McKelvey et al. 1980), and a nemertean egg predator (Botsford and Hobbs 1995). As different model assumptions led to different expected periods of the limit cycles, McKelvey et al. (1980) used this single characteristic to differentiate biological causes. McKelvey et al. (1980) suggested that density-dependent fecundity was the cause of the cycles because it produced cycles with periods of 10–11 years, whereas cannibalism models tended to produce shorter periods of ~8 years (McKelvey et al. 1980; McKelvey and Hankin 1981). However, such conclusions are weakened by the fact that there is no empirical evidence that density-dependent fecundity even exists, whereas there is empirical evidence of both the nemertean worm and female cannibalism influencing dynamics (Botsford and Hobbs 1995).

Analyses of environmental forcing as a cause of the cycles have primarily been statistical assessments of covariability between indicators of recruitment (usually the catch record) and various indicators of the ocean environment. Variables correlated with the catch record include an upwelling index (Peterson 1973; Botsford and Wickham 1978), ocean temperature (Wild 1980), sunspots (Love and Westphall 1981), wind transport (Johnson et al. 1986), and alongshore geostrophic flow (McConnaughey et al. 1992). McConnaughey et al. (1992) also examined the effects of alongshore transport on settlement data. With the exception of sunspots, it is likely that these environmental variables covary with each other in the California Current.

The dominant species of Pacific salmon in the California Current are anadromous and semelparous. Chinook salmon life history varies along the coast (Healey 1991). They can be ocean type, with smolts entering the ocean early in life, or stream type, with juveniles spending more time in the freshwater environment. Spawning ages vary from 3 to 6 years (Healey 1991). Where spawner and recruit data are available, they indicate density dependence, but most often not dramatic overcompensation (e.g., Myers et al. 1995). Artificial propagation contributes substantially to salmon populations. Most stocks of chinook have been harvested, though harvesting has been reduced in some stocks because of consideration for native harvests and the U.S. Endangered Species Act.

Environmental influences on chinook and other Pacific salmon have been assessed for several decades. The critical stage of greatest environmental influence is believed to be the first month after ocean entry, but effects at later ages are also important (Pearcy 1997). Warm ocean conditions that occur during periodic El Niño events and are associated with lower upwelling in the California Current have been found to negatively affect chinook salmon survival and growth (Kope and Botsford 1990), driving poor chinook recruitment in the Northeast Pacific.

The general view of annual effects of climate on marine populations has changed in recent years with the increasing

© 2003 NRC Canada

appreciation of long-term changes and occasional very good or very bad years (Francis et al. 1998). An example of the latter was the observation that the year 1981 was a good year for recruitment to a number of west coast groundfish species (Hollowed and Wooster 1992). Hollowed and Wooster (1992) also identified other years that appeared to be years of good recruitment for a number of California Current species, and they noted that those years were seldom followed by another good year. Several investigators have also noted periodic shifts (termed "regime shifts") in salmon production in the Northeast Pacific, the most recent being associated with an increase in salmon productivity in the Gulf of Alaska in the mid-1970s (Beamish and Boullion 1993; Hare and Francis 1995). The physical oceanographic manifestation of this most recent regime shift is an increasing number of warm-water El Niño years (Francis et al. 1998; McGowan et al. 1998; Timmerman et al. 1999). The biological consequence was proposed to be lower salmon survival in the California Current system and higher salmon survival in the Alaska Current system (Pearcy 1997). It is interesting to note that these climatic influences or environmental forcing factors have characteristic periodicities ranging from a few years (El Niños) to tens of years (decadal regime shifts).

The findings of Hollowed and Wooster (1992) show that the population dynamics of some species critically depend on the frequency of good and bad recruitment years. This indicates that the response of populations to static changes in mean survival may not be an adequate characterization of population dynamics. Further, it increases the importance that we attach to the way in which populations respond to environmental variability acting on different time scales, the focus of this paper.

Models

As we are interested in how physical processes on different time scales influence the population dynamics of species with different life histories, we require two model components. First, we require an environmental forcing function that approximately describes the dominant physical processes and their influence on population dynamics. Second, we require an age-structured model that enables us to describe the timing of various population responses to environmental variability, as determined by the life history traits of the populations. Because our intention in this paper is to highlight the general repercussions of the salient differences between salmon and crab life histories, our modeling strategy is less concerned with precise values of population parameters. We have therefore formulated idealized models of a crab and a Pacific salmon population (e.g., chinook salmon) that differ primarily in one area, the nature of density-dependent recruitment. The results that follow are not dependent on this exact set of parameters; rather, they are dependent on the nature of one parameter — the degree of overcompensation.

Age structure and life history

Here, we use the following age-structured model that uses a Shepherd stock–recruitment function (because the Shepherd formulation can depict a range of characteristics from under- to over-compensation in the stock–recruitment curve):

$$(1)\qquad N_{1,t+1} = \frac{\sum_{i=m}^{L} p_i N_{i,t}}{\frac{1}{r_t} + \left(\frac{\sum_{i=m}^{L} p_i N_{i,t}}{K}\right)^{\gamma}}$$

$$N_{i,t+1} = (1 - H_i)s_i[1 - f(p_i)]N_{i,t}$$

where r_t is the maximum attainable recruitment per unit of biomass (i.e., density-independent portion of the stock–recruitment relationship), K is the threshold biomass beyond which the population becomes dominated by density-dependent processes, and γ is the degree of compensation in the model ($\gamma = 1$ returns the familiar Beverton and Holt model; $\gamma > 1$ is similar to the Ricker model; $\gamma < 1$ gives undercompensation). Further, s_i is the survival from age t to $t + 1$ for cohorts of age i, p_i is the proportion spawning at age i, m is the minimum age at maturation, L is the maximum age class, H_i is the harvest rate of age class i, and $f(p_i)$ is equal to p_i when we are considering a semelparous life history or $f(p_i)$ is equal to 0 if we are considering an iteroparous life history. System 1 isolates r_t as a density-independent term that varies through time. This is intended to represent variability in ocean survival that occurs in the larval stage for Dungeness crab and just after ocean entry for chinook salmon.

The basic life history parameter values used in this paper are listed in Table 1. As alluded to in the previous section, we assume throughout this paper that the Dungeness crab is capable of a strongly overcompensatory stock–recruitment relationship; therefore, γ is likely much greater than 1. We further assume a harvest rate of 0.40, although harvest strategies differ by species. Only male Dungeness crabs that have a carapace width of 159 mm or greater are harvested. For both species, we follow just the females and assume that recruitment in males and females are equal. Therefore, H_i in system 1 is 0 in Table 1 for the Dungeness crab, reflecting the fact that the females are not culled.

To interpret potential influences of large-scale physical processes, we examine variability in the catch data for both Dungeness crab and chinook salmon. Assuming that recruitment occurs at age 4, we can glean point estimates of recruitment from the following simplified stock–recruitment relationship:

$$(2)\qquad N_{R,t} = \rho N_{R,t-4}$$

where $N_{R,t}$ is recruitment at time t and $N_{R,t-4}$ is taken as a proxy for stock size at time $t - 4$ (recall that 4 is assumed age at catch). Here the parameter ρ is similar to the parameter r from system 1 but reflects recruitment to the age-4 cohort per unit of adult biomass. The assumption of density independence allows us to assess the maximum rates of increase in r from the ρ values, although this approach likely

© 2003 NRC Canada

Table 1. Parameters for model system 1 for the two different life histories considered.

Parameters	Chinook salmon	Dungeness crab
m	3	3
L	5	7
s_i	0.80	0.80
H_i	$H_2 = 0.0$	0.0 (females)
	$H_3 - H_5 = 0.40$	
γ	1.0	>1.0
r	0.0–40.0	0.0–40.0
p_i	$p_3 = 0.25$	$p_i = 1.0$
	$p_4 = 0.75$	
	$p_5 = 1.0$	
$f(p_i)$	$f(p_i) = p_i$	$f(p_i) = 0.0$
K	1.0	1.0

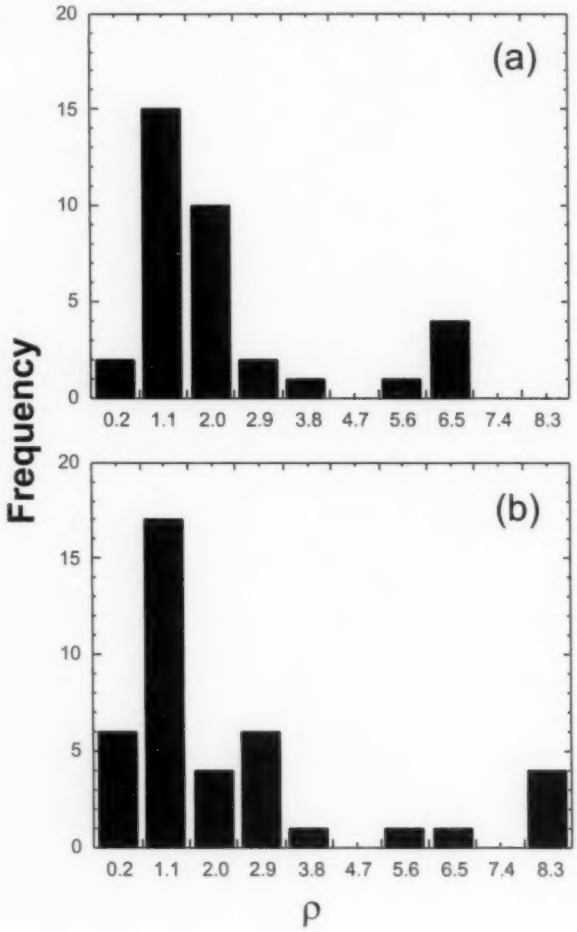
Note: The density-independent portion of the Shepherd function is defined over a range as determined from data used in Fig. 1. We assume that climatic forcing directly influences this parameter. The density-independent portion of the Shepherd function is defined over a range as determined from data used in Fig. 1. We assume that climatic forcing directly influences this parameter.

underestimates r because density dependence influences recruitment. Effectively, this approach allows us to approximate the distribution in environmental variability in recruitment by estimating the range in potential r values experienced in these marine systems. There are two noteworthy patterns in the distribution of estimates of ρ for the stock–recruitment relationship from catch data taken at Eureka and Crescent City, Calif. (Fig. 1). Firstly, the distributions are lognormal (i.e., skewed towards low ρ values). Secondly, the data appear to be characterized by generally weak recruitment events with infrequent pulses of good years (Fig. 1). Here, we are assuming that the two modes (Fig. 1) are related to good recruitment conditions (i.e., large ρ) or bad recruitment conditions (i.e., low ρ). Catch records other than chinook salmon and Dungeness crab on the Northeast Pacific show similar patterns. This is consistent with the general practice of representing recruitment variability as a lognormal variable and is also consistent with characteristics of specific Northeast Pacific groundfish populations identified by Hollowed and Wooster (1992).

In this paper, we use two simple models to describe the variation in recruitment as attributed to underlying physical processes. As we are interested in how populations respond to dominant periodicities in the physical environment, we use a periodic model to reflect this periodicity as well as a stochastic model with a specified mean equal to the period between good years. Additionally, we assume that the physical process directly influences the density-independent portion of recruitment, r (i.e., ocean survival). Consistent with the distributions shown in Fig. 1, we assume that for the most part, recruitment is relatively weak with infrequent pulses of good years.

To set the model within a biologically plausible realm, we translate the ρ values into approximate values of r from system 1. For example, in the case of the chinook salmon, if we assume that all recruitment occurs at age 4, then we get the following relationship:

Fig. 1. Frequency distribution of recruitment strength (ρ values from eq. 1) as estimated from the catch records at Current City, Calif., for (*a*) Dungeness crab (*Cancer magister*) and (*b*) chinook salmon (*Oncorhynchus tshawytscha*).



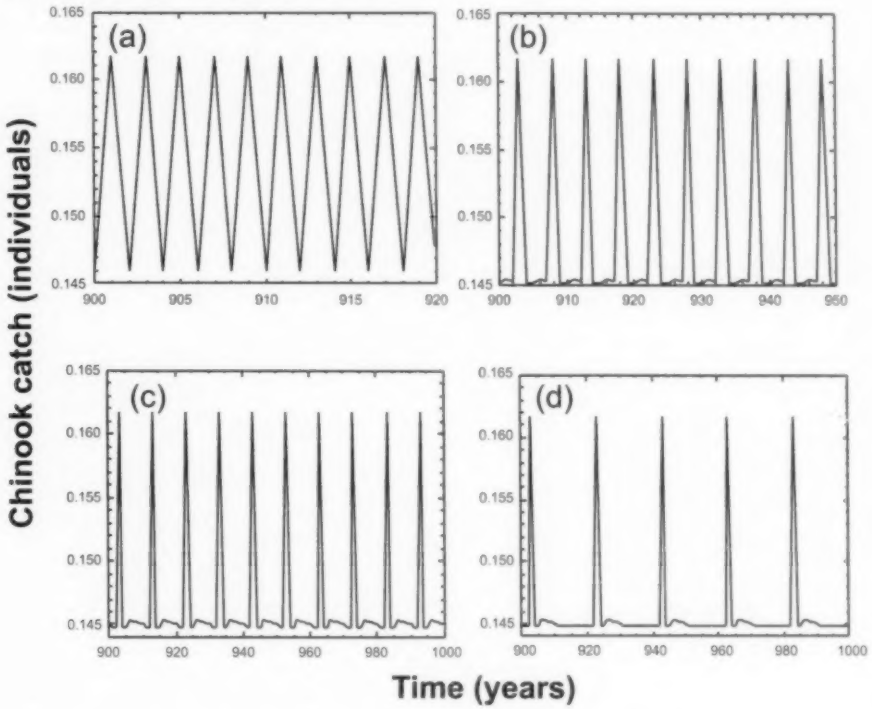
$$r = \frac{\rho}{s_A^3(1 - H)} \quad (3)$$

where s_A is the survivorship in the adult cohort (assumed independent of age class). Using the parameters in Table 1, then r can be estimated to span a maximal range in values from $r \approx 0.0$ (corresponding to $\rho \approx 0.0$) to $r \approx 40.0$ (corresponding to $\rho \approx 8.0$). A similar range in r values can be derived for the Dungeness crab (Higgins et al. 1997). Although this method of estimating r is crude, it is an adequate method for estimating the range that r spans for both species.

The results, which follow, are not sensitive to the exact values in r, only to the fact that a significant difference between good and bad recruitment years exists. For simplicity, we model the variability in recruitment using discrete values of r. We do this by letting r_G embody a good recruitment

© 2003 NRC Canada

Fig. 2. Model solutions after a transient of 900 years for the chinook salmon (*Oncorhynchus tshawytscha*) type life history (r_{AVE} = 4.0, r_G = 40.0, γ = 1.0, s_i = 0.80, K = 1) under four different periods of the climatic forcing function (eq. 3). The solid curves show catch values under the four following periods of the environmental forcing function: a good recruitment year occurs (*a*) every 2 years; (*b*) every 5 years; (*c*) every 10 years; and (*d*) every 20 years.



years and r_{AVE} represent normal recruitment years. Hence, for the periodic model with period τ, we have the following:

$$r_t = r_G \quad \text{if } t/\tau = 1 \tag{4}$$

$$r_t = r_{AVE} \quad \text{if } t \neq 1 \tag{5}$$

where τ is any positive integer value. Similarly, for the stochastic forcing model, we use a point process defined as follows:

$$r_t = r_G \quad \text{if } \varepsilon_t \leq \lambda \tag{6}$$

$$r_t = r_{AVE} \quad \text{if } \varepsilon_t \neq \lambda \tag{7}$$

where λ is the mean of a Poisson process and ε_t is a random number drawn at time t from a uniform distribution on the unit interval. Therefore, λ is the expected frequency of good recruitment years and is inversely related to the period τ of eq. 4 (i.e., $\lambda = 1/\tau$). The use of the periodic forcing function enables analytical insight and aids in the interpretation of our results in the stochastic setting.

We have chosen to investigate a purely periodic forcing function of recruitment (eqs. 4 and 5) and a purely stochastic forcing function of recruitment (eqs. 6 and 7). In what follows, we will compare the results of the purely periodic forcing case (with period τ) with the results of the stochastic model with the same mean time between good recruitment events (i.e., $\tau = 1/\lambda$). The two scenarios can be envisioned as endpoints in terms of recruitment dynamics (from purely periodic signals to purely stochastic signals). Other model choices (e.g., autoregressive process) represent intermediate combinations of stochasticity and periodicity and are relevant; however, we use the two endpoints to show that the results that follow are robust across the spectrum of recruitment dynamics. Intermediate forms of recruitment dynamics (i.e., some combination of the purely stochastic and purely periodic) give consistent results.

Model results

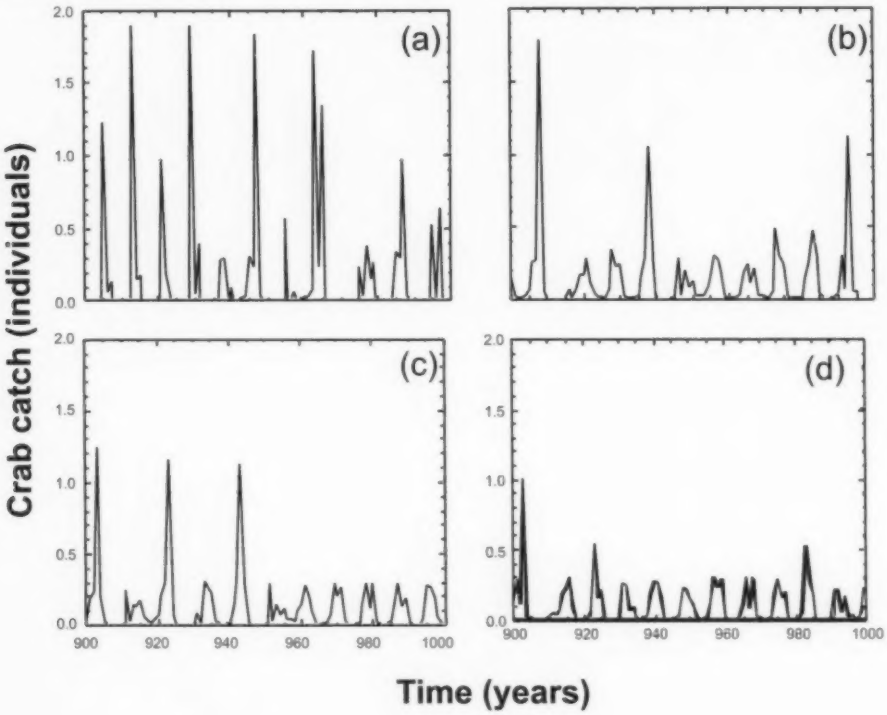
Periodic climatic forcing

Here, we start by discussing the influence of the periodic forcing function (eqs. 4 and 5) on system 1. We find that we get two qualitatively different responses to the periodic environmental influences under the two different life histories (Table 1). To understand these differences in species response, we investigate the influence of periodic forcing as a function of the compensation parameter (γ).

The population trajectories of predicted chinook salmon catch are shown after a transient of 900 years under four different environmental forcing periods (solid curves in Figs. 2*a*–2*d*). In all cases, we assume that r_{AVE} = 4.0 and r_G = 40.0. The qualitative results are robust to large changes in these r values but our choice reflects the data represented in Fig. 1, while additionally ensuring that we are dealing with persistent populations (i.e., positive densities on the systems attractor). Immediately one can see that the period-

© 2003 NRC Canada

Fig. 3. Model solutions after a transient of 900 years for the Dungeness crab (*Cancer magister*; $r_{AVE} = 4.0$, $r_G = 40.0$, $\gamma = 5.0$, $s_i = 0.80$, $K = 1$) under four different periods of the climatic forcing function (eq. 3). The solid curves show catch values under the four following periods of the environmental forcing function: (*a*) a good recruitment year occurs every 2 years; (*b*) every 5 years; (*c*) every 10 years; and (*d*) every 20 years.



icity in the population dynamics matchs the environmental periodicity. The population is responding directly to the good pulses with a delay equivalent to the age at maturation, *m*. The longer period between good pulses (Figs. 2*c*, 2*d*) also show evidence of oscillatory decays with pulses of good recruitment on the order of every 4 years (this is the modal age of spawning in the chinook model). We will find later that these decaying trajectories, on the order of the age structure (3–5 years for chinook), also play a role in the stochastic version of this model. They are essentially a manifestation of the "echo effect" in demography (e.g., Kohlhorst et al. 1991).

The Dungeness crab dynamics do not necessarily mimic the periodicity of the environmental forcing (Figs. 3*a*–3*d*). In fact, for the case presented here ($\gamma = 5.0$), they do not follow this scheme for any forcing period (Figs. 3*a*–3*d*). Instead, the dynamics are quite variable, as the periodicity of the underlying age-structured model interacts in a complex fashion with the periodicity of the environment. Interestingly, the overall periodicity of this form of dynamics remains similar. In all cases here the interaction gives a driving period of about 8–12 years (Figs. 3*a*–3*d*).

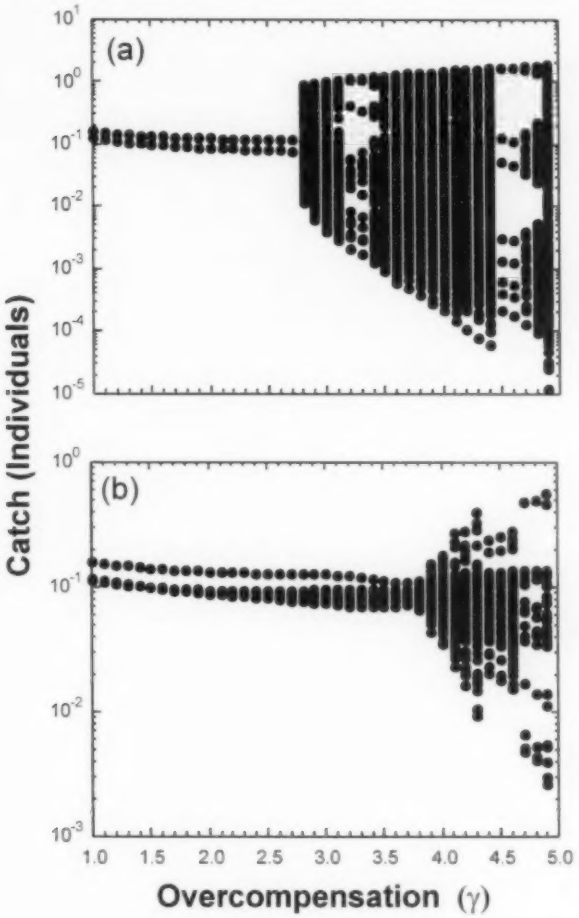
Intuitively, it is relatively easy to understand this latter result. Effectively, the overcompensation acts to filter out good recruitment years that occur within 7 years of each other. Why? Once a strong cohort is recruited into the adult age class (i.e., after *m* years), it immediately acts to suppress other good cohorts from materializing (via density dependence). Clearly, this remains as long as the strong cohort persists in the age structure. Once the pulse of high adult densities moves through the age structure, the population is poised to respond to the next good recruitment event. This drives a filter that tends to occur with a frequency greater than the length of the age structure, *L* (Figs. 3*a*–3*d*). For this result to occur, however, the age classes that suppress recruitment must experience relatively good survivorship (Hastings 1984) — in other words, the population must have a substantial enough adult abundance to drive a strong density-dependent effect.

There is one further result worth mentioning here that is not immediately apparent in Fig. 3. It is possible that as the period of the environmental forcing function increases, we can end up with dynamics in the Dungeness crab similar to that of the chinook population, that is, the dominant frequency of the population dynamics can match the forcing frequency. This occurs simply because the frequency of good events is so low that the last good cohort has already passed through the age structure and so large cohorts do not tend to filter out potentially good recruitment events (via some form of strong density dependence).

In Appendix A, we prove that for the case with an exactly compensating stock–recruitment relationship, the solution must follow the periodicity of the underlying forcing function. The result cannot be extended to the overcompensatory

© 2003 NRC Canada

Fig. 4. Bifurcation diagrams for solutions on the attractor to model system 1 for a range in the degree of recruitment compensation, γ. Catch densities associated with a specific value of γ indicate the year-to-year variation in catch under the following different periods of environmental forcing: (*a*) τ = 2 years; (*b*) τ = 20 years.



case. Effectively, with overcompensation, we move into a situation in which complex dynamical phenomena can arise (e.g., Hastings and Constantino 1991). As overcompensation increases, model system 1 can take on periodic to chaotic dynamics. Therefore, in this latter case, we are potentially coupling oscillators (i.e., the periodic forcing function with an age structure driven oscillator). As is well known, this coupling is a recipe for complex dynamics.

We can examine the influence of overcompensation, γ, by plotting bifurcation diagrams under a number of different environmental forcing frequencies. Here, the bifurcation diagram is a plot of local maxima of the catch in a time series, after a transient of 1000 years, for each value over a range in the overcompensation parameter (Fig. 4). This figure, therefore, depicts solutions to model system 1 over a range in the overcompensation parameter γ under different environmental periodicities for parameters of the crab-type life history (Figs. 4*a*, 4*b*). For heuristic purposes, we can break these figures into two phases. In the first phase (e.g., until about γ = 3.0; Fig. 4*a*), the solution is a relatively simple periodic solution (i.e., one local minima and one local maxima). However, in the second phase (e.g., γ > 3.0; Fig. 4*a*), the solution becomes more dynamically complex as the age structure driven periodicity mixes with the climatic forcing periodicity. In general, as the period in the environmental forcing function increases (e.g., Fig. 4*b*), the dynamics of the solution remain in the first phase until the overcompensation parameter has greater values. At large enough periods, the bifurcation curve will reflect the dynamics of the unforced model as the overcompensation parameter γ is varied — a case that is well studied (e.g., Higgins et al. 1997).

In summary, we see that environmental forcing drives complex dynamics when the abiotic component excites an overcompensatory model. This complex response is excited more readily when the environmental forcing function has a short period between good recruitment events.

We can better understand each of these phases by comparing the period of the environmental forcing function with the dominant period of the population dynamics. We show the phase *i* type population dynamics (γ = 2.50) over a range in environmental forcing periods (Fig. 5*a*). We see that the dominant period of the population dynamics tends to match the environmental period. Clearly, harmonics and subharmonics of this forcing period, τ, will also manifest in the population dynamics (e.g., 1/2τ, 2τ, 3τ,...). These results are consistent with the patterns of chinook dynamics found (Figs. 2*a*–2*d*). This result remains true for all values of γ that display phase-*i* dynamics.

The dynamics response of overcompensatory populations to a range of different forcing periods was similarly explored (γ = 4.50; Fig. 5*b*). In this case, the main period of the population dynamics does not simply mirror the environmental periodicities. Instead, the dominant period lies consistently between 8 and 12 years. These are the Dungeness crab type dynamics that we illustrated (Figs. 3*a*–3*d*). Here, periods less then 8 years are effectively filtered out. Interestingly, this result is very robust, showing dominant periods in the 8- to 12-year range over a substantial range in environmental forcing periodicities. However, at a large enough forcing period, the solutions obviously begin to behave like the unforced model.

Stochastic forcing

To investigate how model 1 behaves under stochastic forcing (eqs. 6 and 7), we re-examined the spectra for a chinook-type life history (Fig. 6) and a Dungeness crab type life history (Fig. 7). The spectra associated with the population time series (solid curve) generated by the stochastic version of the chinook model under three different mean forcing periodicities (λ = 3, 5, and 7 years) were examined (Figs. 6*a*–6*c*, respectively). The dashed curve is the spectrum generated by the environmental noise (i.e., r_t). As with similar stochastic linear processes, the mean frequency, λ, does not dominate the spectral signal (dashed curve), instead the climatic signal is relatively uniform — a characteristic of a white noise spectral signal. Note, though, that the stochastic

© 2003 NRC Canada

Fig. 5. The dominant period of the population dynamics (corresponding to the strongest component of the spectral analysis for frequencies above 0.01) are compared with the underlying environmental forcing period. (*a*) The relationship between the Chinook-type (phase *i*, $\gamma = 2.50$) population dynamics and the environmental forcing period. Here, the dominant period of the population dynamic matches the environmental forcing period. (*b*) The relationship between the Dungeness crab type (phase *ii*, $\gamma = 4.50$) population dynamics and the environmental forcing period. Here, the population dynamics robustly produce dominant periodicities of 8–12 years.

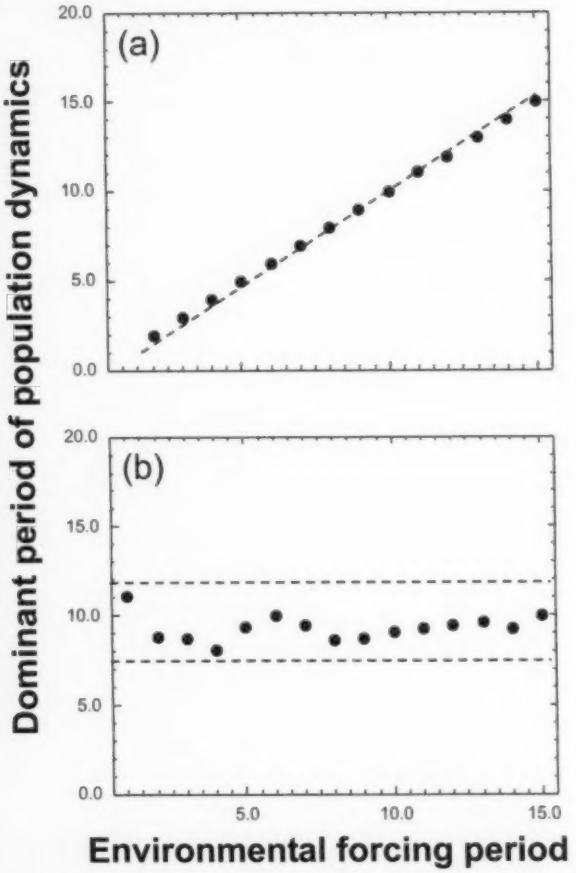
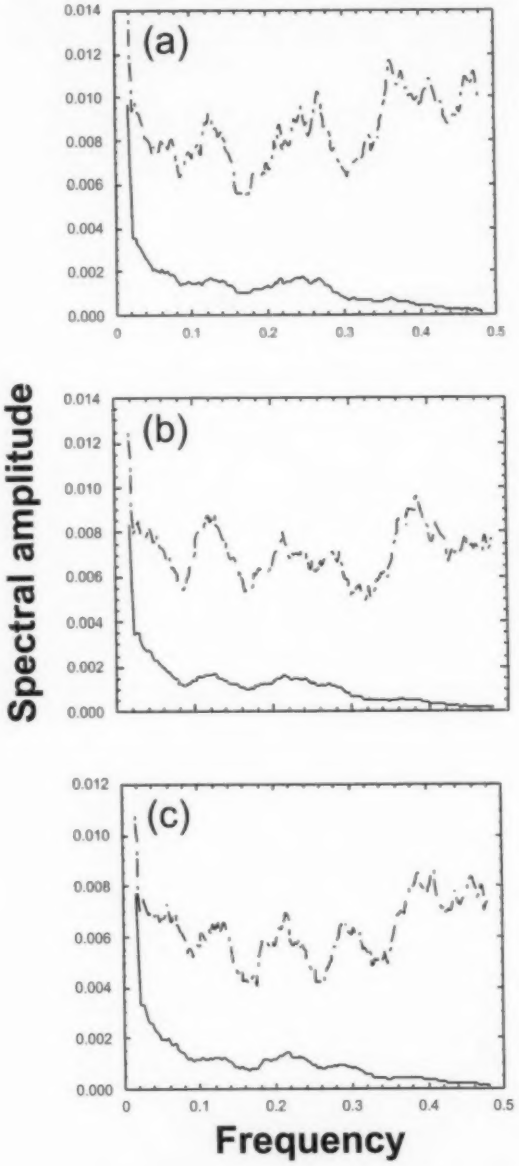


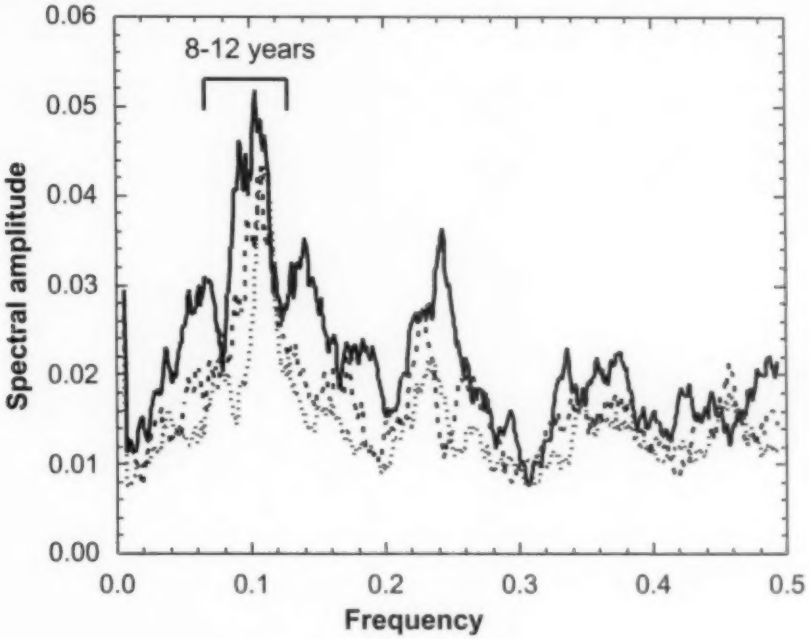
Fig. 6. Spectral amplitude (running average over 20 points) for the chinook salmon (*Oncorhynchus tshawytscha*) population dynamics (solid curve) and the underlying stochastic climatic forcing function (dashed curve) for three different mean forcing periodicities: (*a*) $\lambda = 3$ years; (*b*) $\lambda = 5$ years; and (*c*) $\lambda = 7$ years.



signal becomes increasingly less influenced by high-frequency fluctuations as the mean period increases (dashed curves in Figs. 6*a*–6*c*). The chinook spectral signal follows this environmental signal closely with one deviation. The spectral signals of the population dynamics show a modest decrease compared with the environmental signal. Although subtle, this is likely a remnant of the echo effect, as the population spectral signal rises slightly over the 0.20–0.30 frequency range (corresponding to a 3- to 5-year life history) and decreases just below and beyond these frequencies. Higher frequencies are increasingly filtered out as the mean period increases (solid curves in Figs. 6*a*–6c) because the age-structured decay increasingly dominates the dynamics and filters out higher frequency stochastic influences. These results are robust for the chinook-type population dynamics. As previously noted, a similar echo effect appeared in the periodic model when the perturbation occurred at reasonably long intervals (e.g., 10 and 20 years; Figs. 2*c*, 2*d*). Because stochasticity ensures that long periods between good recruitment events will exist, at least infrequently, then the transient oscillatory decay will influence stochastic dynamics to some extent by filtering out higher frequency stochastic

© 2003 NRC Canada

Fig. 7. Spectral amplitude (running average over 20 points) of population dynamics for the Dungeness crab (*Cancer magister*) or overcompensatory dynamics under a range in mean forcing frequencies (λ = 3 years, dashed curve; λ = 5 years, solid curve; and λ = 7 years, dotted curve).



fluctuations. Therefore, somewhat surprisingly, a hint of age structure induced oscillations may even occur in a species with exactly compensating recruitment biology. Some recent research has found such age-structured oscillations (Myers et al. 1998; Stenseth et al. 1999). For example, Myers et al. (1998) recently found similar results for sockeye salmon subjected to stochastic forcing (white noise) and predicted spectral signals peaking in this range of frequencies.

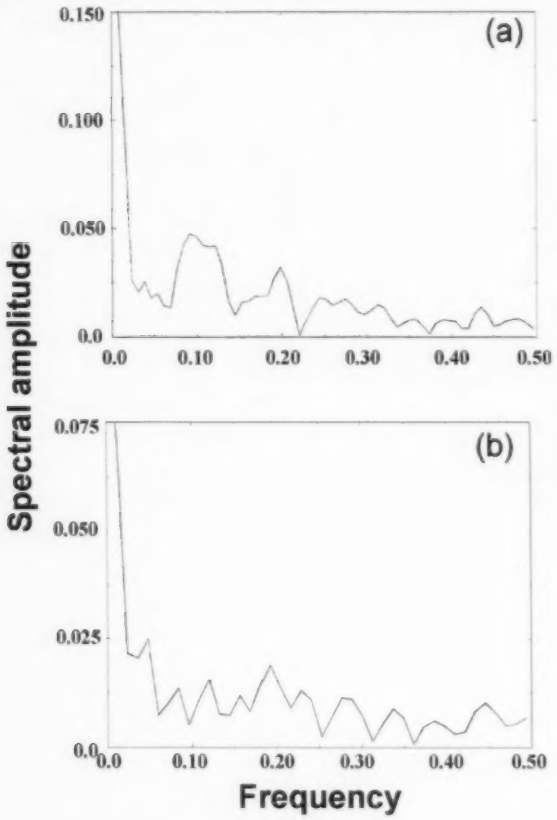
As with the periodic case, the stochastically forced population dynamics of the Dungeness crab case (i.e., overcompensatory recruitment) behave differently than the compensatory case dynamics. The spectral signals associated with the population time series generated by the stochastic version of the Dungeness crab model under three different mean forcing periodicities (λ = 3, 5, and 7 years; dashed, solid, and dotted curves in Fig. 7, respectively) were again examined (Fig. 7). The results show that for a range in mean forcing periodicities, the Dungeness crab population dynamics have a dominant periodicity that lies between 8 and 12 years (0.08–0.125 cycles·year^{-1} in Fig. 7). Here, the strong density dependence (overcompensation) is filtering out potentially good recruitment events whenever these good conditions lie within 7 years of each other (i.e., the age structure). The result is that the mean driving periodicity is necessarily skewed towards values greater than 7 years. Because periodicities below 8 years are muted, the spectral signal takes on the appearance of a large tooth over the range from 8 to 12 years (0.08–0.125 cycles·year^{-1} in Fig. 7). The existence of good and bad recruitment events is critical to this result. Subtleties, though, on our stochastic structure beget the same result. For example, had we used good, bad, and average recruitment years in our model, then the qualitative results would still hold.

This is an intriguing example of how nonlinearities can be of great importance in interpreting the influence of stochastically varying environments (see also Ranta et al. 2000; Laasko et al. 2001). Using a general model formulation, Laasko et al. (2001) warned that biological processes might act to filter out environmental signals. Here, we have found that strong density dependence that materializes in the Dungeness crab life history (e.g., cannibalism) acts as a filter on important abiotic processes (e.g., El Niño). Specifically, stochastic environments with a long mean time between good environmental conditions (>>8 years) will tend to give a driving periodicity in the population dynamics that approaches that of the unforced dynamics (e.g., generally 8 years for the Dungeness crab; see Botsford and Hobbs 1995). Although shorter climatic forcing periods, like those on the scale of the El Niño Southern Oscillation (ENSO; 3–7 years), tend to drive periods closer to 10 years. The result suggests that the 10-year periodicity found in the data may be a combination of the age-structured density dependence interacting with the period of the climatic forcing. The period of ENSO events (3–7 years) is consistent with the hypothesis that ENSO is the driving environmental forcing function behind Dungeness crab population dynamics.

The patterns in the spectra of the two different exploited marine populations can be used to interpret data from catch records (Fig. 8). The spectra are determined from 30 years of catch data for the Dungeness crab (Fig. 8*a*) and the chinook salmon (Fig. 8*b*) at Crescent City and Eureka, Calif. Both signals are consistent with the model predictions. The

© 2003 NRC Canada

Fig. 8. Spectral magnitude (power) of Dungeness crab and chinook salmon catch records from Current City, Calif. (*a*) The Dungeness crab (*Cancer magister*) spectral signal is peaked around 10 years (0.10 cycles·year^{-1}), consistent with model results, whereas (*b*) the chinook salmon (*Oncorhynchus tshawytscha*) spectral signal is reddened.



Dungeness crab shows the "large tooth" in spectral amplitude consistent with the stochastic model, corresponding to oscillations on the order of a decade. The chinook signal, on the other hand, is more uniform, with a modest peak near 0.20 (perhaps a remnant of age structure driven oscillations with a mean adult age of ~5 years). Interestingly, Myers et al. (1998) found similar results for sockeye salmon and independently suggested the same mechanism. Although other mechanisms may be operating, the predictions provide an enticing match to the data and warrant further investigation.

Discussion

The models that we use in this paper allow us to investigate the influence of variability in the frequency of good recruitment events in an otherwise harsh world. Many fish biologists have argued that recruitment in fish populations can be viewed in this simple manner as recruitment data having the tendency to be dominated by few good recruitment events (Hollowed and Wooster 1992).

We have found that nonlinearities arising in the recruitment biology of a population are important in interpreting the influence of climatic forcing on population dynamics. This area of research is a relatively unexplored issue in ecology, although recently theory is beginning to emerge. Consistent with our findings is the general notion that density-dependent feedback plays a central role in the response of the population dynamics to environmental forcing (Ranta et al. 2000; Kaitala and Ranta 2001). Here, we find that exactly compensatory, or relatively weakly overcompensatory, recruitment relationships like those found for the chinook and coho salmon are likely to respond directly to climatic forcing, although it is possible that these also display periodicities set by their age structure (see also Myers et al. 1998; Stenseth et al. 1999). On the other hand, the response to climatic forcing by species with overcompensatory recruitment relationships, like those that arise in the Dungeness crab, are not so direct. The density dependence, in this case, is extremely robust to the climate forcing, and hence, the age structure driven oscillations tend still to play a strong role in dynamic outcomes. Effectively, the density dependence acts as a filter to recruitment events that occur on a temporal scale less than the time it takes for a strong cohort to work its way through the age structure. Further, this filter tends to interact with stochastic environmental forcing to increase the mean of the driving period (i.e., the peak in the spectral analysis) in the dynamics. This occurs because the overcompensation filters out (i.e., suppresses) periods less than the maximal substantial age class in the age structure (for Dungeness crab, ~8 years) but not longer periods. The mean driving frequency is thus skewed towards lower frequencies (<0.125) and higher periods (>8 years). These results agree with the estimated periods from Dungeness crab catch data. Recent work by Bjornstad et al. (1999) has found that strong intercohort density dependence in cod on the Norwegian coast coupled with environmental variability induce complex dynamics that resonate with both short- and long-term fluctuations. It appears that at least some species are capable of incurring such strong density-dependent influences across cohorts.

From a scientific perspective, these results better inform investigators of the causes of population variability. When attempting to determine the cause of population fluctuations, there is a tendency to look for environmental time series with dominant variability at the same time scale as the time series of population variability (Ranta et al. 2000). Results obtained here indicate that a population can be forced by an environmental variable but not exhibit the same frequency of variability. In an interesting contribution, Pascual and Ellner (2000) showed that dominant climatic periods might be able to be deciphered from biotic signals using nonlinear, nonparametric time-series approaches. They tested their approach using two species predator–prey models. Further development in this area could prove very useful in disentangling the biotic and abiotic contribution to population dynamics.

From a management perspective, this suggests that fishery quotas for certain species, like the chinook salmon, should seriously consider climatic indices that correspond to recruitment success (e.g., upwelling indices). However, for other species like the Dungeness crab (and the Norwegian

© 2003 NRC Canada

cod; Bjornstad et al. 1999), this connection is more tenuous. Quotas for exploited marine populations of this type are better managed if the quotas are structured from climatic indices that reflect "potential" recruitment success and estimates in the density of the population age structure. In the case of the Dungeness crab, this would require an estimate, or an index, of the female densities. If these densities are high, then a good upwelling year will not necessarily imply a good recruitment of males into the fishery 3–4 years later. In fact, we can expect the opposite and should manage the population accordingly.

Finally, our results have implications for population behavior in response to changes in the frequency of warm-water El Niño events in the Northeast Pacific. Global climate change models have predicted an increase in the frequency of ENSO events (Timmerman et al. 1999), and paleological records from coral cores indicate that the frequency of ENSOs has varied in the past. Because increased frequencies in El Niño events imply a decrease in the frequency of good recruitment events, then our models suggest that population dynamics will change in a predictable way. That is, assuming all other things equal, a decreased frequency in good recruitment conditions implies that Dungeness crab should begin to experience lower driving periodicities with a tendency for a decreasing amplitude in population spikes that corresponds to good recruitment events. Chinook and coho salmon should also begin to experience lower driving periodicities and a decrease in the amplitude of the population spikes that correspond to good recruitment events. Additionally, we would expect Pacific salmon to begin to take on more pronounced oscillations corresponding to their age structure (e.g., 3–6 years for the chinook) before a population crash. It is dangerous to assume that because a population is occasionally rebounding (here, because of infrequent good environmental conditions), this implies a relative invulnerability to local extinction. In fact, weak oscillatory decays with a driving frequency that matches the age structure can be indicative of populations moving into dynamical regimes with a high probability of extinction. This line of investigation is preliminary and somewhat speculative but is consistent with the models investigated here.

In summary, these results illustrate that populations may not always respond to environmental variability by simply tracking changes, especially if the variability is on time scales near the maximum age in the population. Complex behaviors can arise that have implications for the detection of environmental forcing, the prediction of future population responses to environmental change, and possibly to fishery management. Clearly, the response to environmental forcing, or the lack thereof, is likely to depend on where the density dependence arises in the life history (Gurney and Nisbet 1985). Therefore, although these results are enticing for strong density dependence in the early life stages, it remains an open area of investigation for life cycles in which the density dependence manifests elsewhere.

Acknowledgements

We thank Dr. James Umbanhowar and two anonymous reviewers for their helpful suggestions. This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) postdoctoral fellowship (K.M.), an NSERC grant (K.M.), and a National Oceanographic and Atmospheric Administration (NOAA) grant (L.B.).

References

Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can J. Fish. Aquat. Sci. **50**: 1002–1016.

Bjornstad, O.N., and Grenfell, B.T. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. Science (Wash., D.C.), **293**: 638–643.

Bjornstad, O.N., Fromentin, J.M., Stenseth, N.C., and Gjosaeter, J. 1999. Cycles and trends in cod populations. Proc. Natl. Acad. Sci. U.S.A. **96**: 5066–5071.

Botsford, L.W., and Hobbs, R.C. 1995. Recent advances in the understanding of cyclic behavior of Dungeness crab (*Cancer magister*) populations. ICES (Int. Counc. Explor. Sea) Mar. Sci. Symp. **199**: 157–196.

Botsford, L.W., and Wickham, D.E. 1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. **35**: 833–843.

Botsford, L.W., Armstrong, D.A., and Shenker, J.M. 1989. Oceanographic influences on the dynamics of commercially fished populations. *In* Coastal oceanography of Washington and Oregon. *Edited by* M.R. Landry and B.M. Hickey. Elsevier, Amsterdam. pp. 511–564.

Collie, J.S., and Spencer, P.D. 1994. Modeling predator–prey dynamics in fluctuating environment. Can. J. Fish. Aquat. Sci. **51**: 2665–2672.

Francis, R.C., Hare, S.R., Hollowed, A.B., and Wooster, W.S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the Northeast Pacific. Fish. Oceanogr. **7**: 1–21.

Gotshall, D.W. 1977. Stomach contents of northern California Dungeness crabs, *Cancer magister*. Calif. Fish Game, **63**: 43–51.

Gurney, W.S.C., and Nisbet, R.M. 1985. Fluctuation periodicity, generation separation, and the expression of larval competition. Theor. Popul. Biol. **28**: 150–180.

Hare, S.R., and Francis, R.C. 1995. Climate ocenaography of salmon production in the Northeast Pacific. *In* Symposium on Climate Change and Northern Fisheries Populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 357–372.

Hastings, A. 1984. Age-dependent predation is not a simple process. II. Wolves, ungulates, and a discrete time model for predation on juveniles with a stabilizing tail. Theor. Popul. Biol. **26**: 271–282.

Hastings, A., and Constantino, R.F. 1991. Oscillations in population numbers: age-dependent cannibalism. J. Anim. Ecol. **60**: 471–482.

Healey, M.C. 1991. The life history of chinook salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. U.B.C. Press, Vancouver, B.C. pp. 311–393.

Higgins, K., Hastings, A., and Botsford, L.W. 1997. Density dependence and age structure: nonlinear dynamics and population behavior. Am. Nat. **149**: 247–269.

Hollowed, A.B., and Wooster, W.S. 1992. Variability of winter ocean conditions and strong year classes of Northeast Pacific groundfish. ICES (Int. Counc. Explor. Sea). Sci. Symp. **195**: 433–444.

Johnson, D.F., Botsford, L.W., Methot, R.D., and Wainwright, T.C. 1986. Wind stress and cycles in Dungeness crab (*Cancer magis-*

© 2003 NRC Canada

ter) catch off California, Oregon and Washington. Can. J. Fish. Aquat. Sci. **43**: 838–845.

Kaitala, V., and Ranta, E. 2001. Is the impact of environmental noise visible in the dynamics of age-structured populations? Proc. R. Soc. Lond. B Biol. Sci. **268**: 1769–1774.

Kohlhorst, D.W., Botsford, L.W., Brennan, J.S., and Cailliet, G.M. 1991. Aspects of the structure and dynamics of an exploited central California population of white sturgeon (*Acipenser transmontanus*). *In* Actes du Premier Colloque Internationale sur l'Esturgeon. *Edited by* P. Williot. CEMAGREF-DICOVA; PB Diffusion, Lavoisier and Boc, Bordeaux, France. pp. 277–294.

Kope R.G., and Botsford, L.W. 1990. Determination of factors affecting recruitment of chinook salmon (*Oncorhynchus tshawytcha*) in central California. Fish. Bull. **88**: 257–269.

Laasko, J., Kaitala, V., and Ranta, E. 2001. How does environmental variation translate into biological processes? Oikos, **92**: 119–122.

Love, M.S., and Westphal, M. 1981. A correlation between annual catches of Dungeness crab, *Cancer magister*, along the west coast of North America and mean annual sunspot numbers. Fish. Bull. **79**: 794–796.

McConnaughey, R.A., Armstrong, D., Hickey, B., and Gunderson, D. 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. Can. J. Fish. Aquat. Sci. **49**: 2028–2044.

McKelvey, R., and Hankin, D. 1981. Reply to comment on cycles in the northern California Dungeness crab population. Can. J. Fish. Aquat. Sci. **38**: 1296–1297.

McKelvey, R., Hankin, D., Yanosko, K., and Snygg, C. 1980. Stable cycles in multistage recruitment models: an application to the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. **37**: 2323–2345.

McGowan, J.A., Cayan, D.R., and Dorman, L.R. 1998. Climate–ocean variability and ecosystem response in the Northeast Pacific. Science (Wash., D.C.), **281**: 210–217.

Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide spawner and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. No. 2024.

Myers, R.A., Mertz, G., Bridson, J., and Bradford, M. 1998. Simple dynamics underlie sockeye salmon (*Oncorhynchus nerka*) cycles. Can. J. Fish. Aquat. Sci. **55**: 2355–2364.

Nisbet, R.M., and Gurney, W.S.C. 1976. Simple mechanisms for population cycles. Nature (Lond.), **263**: 319–320.

Pascual, M., and Ellner, S.P. 2000. Linking ecological patterns to environmental forcing via nonlinear time series models. Ecology, **81**: 2767–2780.

Pearcy, W.G. 1997. Salmon production in changing ocean domains. *In* Pacific salmon and their ecosystems. *Edited by* D.J. Stouder, P.A. Bisson, and R.J. Naiman. Chapman & Hall, New York.

Peterson, W.T. 1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull. **71**: 902–910.

Ranta, E., Lundberg, P., Kaitala, V., and Laasko, J. 2000. Visibility of the environmental noise modulating population dynamics. Proc. R. Soc. Lond. B Biol. Sci. **267**: 1851–1856.

Steele, J.H., and Henderson, E.W. 1984. Modeling long-term fluctuations in fish stocks. Science (Wash., D.C.), **224**: 985–986.

Stenseth, N.C., Bjornstad, O.N., and Falck, W. 1999. Dynamics of coastal cod populations: intra- and intercohort density dependence and stochastic processes. Proc. R. Soc. Lond. B Biol. Sci. **266**: 1645–1654.

Timmerman, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M., and Roeckner, E. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature (Lond.), **398**: 694–697.

Wainwright, T.C., and Armstrong, D. 1993. Growth patterns in the Dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models. J. Crust. Biol. **13**: 36–50.

Wild, P.W. 1980. Effects of seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungness crab, *Cancer magister*. Calif. Coop. Ocean. Fish Investig. Rep. **XXI**: 115–120.

Appendix A

Here, we prove that the exactly compensatory case of system 1 under periodic forcing has a period that is either exactly equal to the period of the physical forcing function or is an integer multiple of the period of the forcing function.

Here we use the following, more general version of system 1:

$$\text{(A1)}\quad N_{1,t+1} = \frac{\sum_{i=m}^{L} \alpha_i N_{i,t}}{\frac{1}{r_t} + \left(\sum_{i=m}^{L} \alpha_i N_{i,t}\right)^{\gamma}} = F_1$$

$$N_{i,t+1} = \sigma_i N_{i-1,t} = F_i$$

$$\vdots$$

$$N_{m,t+1} = \sigma_m N_{m-1,t} = F_m$$

where m is age at maturation; L is age of senescence; α_i is the proportional contribution of age class i to recruitment; σ_i is survival from age $i - 1$ to i; compensation, γ, is the compensation parameter and is set to 1 (i.e., the exactly compensatory case); K has been scaled to 1; and r_t is governed by the periodic forcing function (eqs. 4 and 5).

Theorem 1: For system A1 with $\gamma = 1.0$ coupled with the periodic forcing function defined by eqs. 4 and 5 with $r_G > r_{AVE}$, all positive solutions have a periodic solution with a period that either is exactly equal to the forcing function (τ) or is some integer multiple, I, of the forcing function ($I\tau$).

Proof

The proof proceeds by first establishing the three properties inherent in system A1: (*i*) that the unforced version of system A1 ($r_t = r$) has a solution that is necessarily bounded within a region of positive values; (*ii*) that given $r_t = r_{AVE}$, all trajectories that lie above the equilibrium associated with r_{AVE} strictly decrease (similarly, given $r_t = r_G$, all trajectories that lie below the equilibrium associated with r_G strictly increase; and (*iii*) that the maximum of the attractor, χ_{MAX}, results from a good recruitment year, r_G, whereas the minimum of the attractor, χ_{MIN}, results from an average recruitment year, r_{AVE}, followed by a good recruitment year, r_G.

From these three properties, we show that Theorem 1 must hold, therefore the solution is being driven by the periodic forcing function — or climatic forcing function — as defined here. Finally, we end by proving the existence, but not uniqueness, of a τ-periodic solution.

© 2003 NRC Canada

Property i: the attractor of eq. A1 is necessarily bounded within a region of positive values.

First, we start by showing that system A1 with a constant r (i.e., $r_i = r$) is globally stable. System A1, after some algebraic manipulation, can be found to have the following positive equilibrium solution:

$$\text{(A2)}\quad E_+ : N_1^* = \frac{\sum_{i=m}^{L} \alpha_i \prod_{j=1}^{i-(m-1)} \sigma_j - \frac{1}{r}}{\sum_{i=m}^{L} \alpha_i \prod_{j=1}^{i-(m-1)} \sigma_j}$$

$$N_i^* = \prod_{j=2}^{i} \sigma_{j-1} N_1^*$$

The positive equilibrium solution exists whenever r is greater then the following relationship:

$$\text{(A3)}\quad r_+ = \frac{1}{\sum_{i=m}^{L} \alpha_i \prod_{j=1}^{i-(m-1)} \sigma_j}$$

Here, r_+ is the transcritical bifurcation point separating the region of positive solutions from negative solutions. A zero equilibrium solution, E_0, also exists where $N_1 = \ldots = N_L = 0$. Later we will show that regardless of this zero solution, all positive initial value problems must evolve to the E_+ equilibrium above.

To determine the local stability properties of the E_+ equilibrium, we determine the eigenvalues of the linearization of system A1, the Jacobian matrix, at the equilibrium defined by eq. A2. The Jacobian matrix can be determined to be

	$\frac{\partial F_1}{\partial N_1}$	$\frac{\partial F_2}{\partial N_2}$	...	$\frac{\partial F_m}{\partial N_m}$	...	...	$\frac{\partial F_L}{\partial N_L}$
$\frac{\partial F_1}{\partial N_1}$	$0-\lambda$	0	0	$\frac{1}{\frac{1}{r}+\sum_{j=m}^{L} N_j^*}\left(1-\frac{N_m^*}{\frac{1}{r}\sum_{j=m}^{L} N_j^*}\right)$	...	...	$\frac{1}{\frac{1}{r}+\sum_{j=m}^{L} N_j^*}\left(1-\frac{N_L^*}{\frac{1}{r}\sum_{j=m}^{L} N_j^*}\right)$
$\frac{\partial F_2}{\partial N_2}$	σ_1	$0-\lambda$	0	0	0	0	0
$\vdots$	0	σ_i	$0-\lambda$	0	0	0	0
$\frac{\partial F_m}{\partial N_m}$	0	0	σ_m	$0-\lambda$	0	0	0
$\vdots$	0	0	0	σ_i	$0-\lambda$	0	0
$\vdots$	0	0	0	0	σ_i	$0-\lambda$	0
$\frac{\partial F_L}{\partial N_L}$	0	0	0	0	0	σ_L	$0-\lambda$

After some algebra, the characteristic polynomial of the Jacobian can be determined:

$$\text{(A4)}\quad p(\lambda) = \lambda^L - \sum_{i=0}^{L-m}\left(\prod_{j=1}^{L-(i+1)} \sigma_j\right) m_{1,L-i}\,\lambda^i$$

where the $m_{1,i}$s are defined as

$$\text{(A5)}\quad m_{1,i} = \frac{\alpha_i}{r\left(\alpha_m + \sum_{j=1}^{L-m} \alpha_{m+j}\left(\prod_{k=m}^{L-1} \sigma_k\right)\right)^2\left(\prod_{h=1}^{m-1} \sigma_h^2\right)}$$

Now to prove that system A1, with a constant r value, is locally stable requires that we prove that all absolute values of the eigenvalues determined from the characteristic polynomial are less than 1. After substituting eq. A5 into the characteristic polynomial (eq. A4), we get

$$\text{(A6)}\quad p(\lambda) = \lambda^L - \frac{\left[\sum_{i=0}^{L=m}\left(\prod_{j=1}^{L-(i+1)} \sigma_j\right)\alpha_{L-i}\,\lambda^i\right]}{r\left(\alpha_m + \sum_{j=1}^{L-m} \alpha_{m+j}\left(\prod_{k=m}^{L-1} \sigma_k\right)\right)^2\left(\prod_{h=1}^{m-1} \sigma_h^2\right)}$$

The eigenvalues are all of the zero solutions to eq. A6. Let us start with the case that r is equal to r_+ (eq. 4), then eq. 6 becomes

$$\text{(A7)}\quad p(\lambda) = \lambda^L - \frac{\left(\sum_{i=m}^{L} \alpha_i \prod_{j=1}^{i-(m-1)} \sigma_j\right)\left[\sum_{i=0}^{L-m}\left(\prod_{j=1}^{L-(i+1)} \sigma_j\right)\alpha_{L-1}\lambda^i\right]}{\left(\alpha_m + \sum_{j=1}^{L-m} \alpha_{m+j}\left(\prod_{k=m}^{L=1} \sigma_k\right)\right)^2\left(\prod_{h=1}^{m-1} \sigma_h^2\right)} = 0$$

© 2003 NRC Canada

Pulling out the $\sigma_1, \sigma_2, \ldots \sigma_{m-1}$ terms from both parts of the numerator in eq. A7 gives the following:

$$\text{(A8)}\quad p(\lambda) = \lambda^L - \frac{\left(\alpha_m + \sum_{j=1}^{L-m}\alpha_{m+j}\left(\prod_{k=m}^{L-1}\sigma_k\right)\right)^2\left(\prod_{h=1}^{m-1}\sigma_h^2\right)\left[\sum_{i=0}^{L-m}\left(\prod_{j=m}^{L-(i+1)}\sigma_j\right)\alpha_{L-i}\lambda^i\right]}{\left(\alpha_m + \sum_{j=1}^{L-m}\alpha_{m+j}\left(\prod_{k=m}^{L-1}\sigma_k\right)\right)^2\left(\prod_{h=1}^{m-1}\sigma_h^2\right)} = 0$$

which reduces to

$$\text{(A9)}\quad p(\lambda) = \lambda^L - \left[\sum_{i=0}^{L-m}\left(\prod_{j=m}^{L-(i+1)}\sigma_j\right)\alpha_{L-i}\lambda^i\right] = 0$$

or, equivalently

$$\text{(A10)}\quad p(\lambda) = \lambda^L - \prod_{j=m}^{L-1}\sigma_j\alpha_L - \prod_{j=m}^{L-2}\sigma_j\alpha_{L-1}\lambda^1\Lambda - \alpha_{L-1}\lambda^{L-m} = 0$$

where each negative term in eq. A10 is composed of an $(L - m + 1)$ multiple (i.e., the number or σs, αs, and the power of λ in each term added to $(L - m + 1)$). Now, if $|\lambda| = 1 >$, then it is true that

$$\text{(A11)}\quad |\lambda|^L > |\lambda|^{L-m} > |\lambda|^{L-m-1} > \quad > |\lambda|$$

We also know that the negative terms in eq. A10 must have the following relationship:

$$\text{(A12)}\quad \left|\sum_{i=0}^{L-m}\left(\prod_{j-m}^{L-(i+1)}\sigma_j\right)\alpha_{L-i}\lambda^i\right| \le \left|\sum_{i=0}^{L-m}\left(\prod_{j-m}^{L-(i+1)}\sigma_j\right)\lambda^i\right| \le |\lambda|^{L-m}$$

because the σs are less then 1 (i.e., λ) > and the αs sum to 1 in eq. A10.

This implies that $|\lambda| > 1$ cannot be a solution to eq. A9. Therefore, for the special case that $r = r_+$, the eigenvalue must satisfy $|\lambda| \le 1$. Now, as r increases beyond r_+ (i.e., all positive solutions to eq. A1), then from eqs. A11 and A6, we know that

$$\text{(A13)}\quad |\lambda|^L > \left|\frac{\left[\sum_{i=0}^{L-m}\left(\prod_{j=1}^{L-(i+1)}\sigma_j\right)\alpha_{L-i}\lambda^i\right]}{r\left(\alpha_m + \sum_{j=1}^{L-m}\alpha_{m+j}\left(\prod_{k=m}^{L-1}\sigma_k\right)\right)^2\left(\prod_{h=1}^{m-1}\sigma_h^2\right)}\right|$$

which implies that $|\lambda| \ge 1$ can't be a solution to eq. A9 and therefore all positive solutions are locally stable (i.e., they lie in the range $|\lambda| > 1$).

To show that all positive initial values evolve to E_+ (i.e., the ω-limit set is $\mathbf{R}_+^L$), we are required to show that sufficiently small positive values, ε_i, near all boundaries increase. For r values beyond r_+ — the values that we are considering here — this is necessarily the case because r ensures positive growth at small magnitudes.

Now we are in a position to show that all solutions to the periodically forced version of system A1 are necessarily bounded in the positive space, $\mathbf{R}_+^L$. Because any constant r produces a globally stable equilibrium solution (in the sense of meaningful biological solutions, $\mathbf{R}_+^L$), then we know that the system through time must eventually end up above the equilibrium, E_{MIN}, associated with the r_{AVE} value in eq. 5. It has to because both r_{AVE} and r_G will pull the trajectories to it (when $r_t = r_{AVE}$) or beyond it (when $r_t = r_G$). Further, we know that the system through time must also evolve to a dynamic that lies below the equilibrium, E_{MAX}, associated with the r_G value in eq. 4, because both r_{AVE} and r_G will pull the trajectories either to it (r_G) or below it (r_{AVE}). Hence, the attractor is bounded in $\mathbf{R}_+^L$ with a minimum value, χ_{MIN}, that is greater then E_{MIN} and a maximum value, χ_{MAX}, that is less than E_{MAX}.

Property ii: Given $r_t = r_{AVE}$, all trajectories that lie above E_{MIN} strictly decrease. Similarly, given $r_t = r_G$, all trajectories that lie below E_{MAX} strictly increase.

We start by considering an initial value problem. That is, we are interested in the dynamic behavior, given $r_t = r_{AVE}$ and initial values such that all N_is lie above the N_is associated with E_{MIN}. Because the dynamics are governed by a monotonically increasing function of adult density (i.e., the recruitment function), then all values that lie above E_{MIN} can only monotonically decrease towards E_{MIN}. A similar argument holds for the case in which $r_t = r_G$ and the initial value lies below E_{MAX}.

Property iii: The maximum of the attractor, χ_{MAX}, results from a good recruitment year, r_G. The minimum of the attractor, χ_{MIN}, results from an average recruitment year, r_{AVE}, followed by a good recruitment year, r_G.

By property *ii*, we know that the maximum of the attractor, χ_{MAX}, could only result from r_{AVE} if it was at a point above χ_{MAX}. This cannot be because then it would be χ_{MAX}. Hence, by contradiction, only r_G could have spawned χ_{MAX}. Further, by definition, r_G is followed by r_{AVE}.

Similarly, by property *ii*, we know that the minimum of the attractor, χ_{MIN}, could only result from r_G if it was at a point below χ_{MIN}. This cannot be because it then would be χ_{MIN}. Hence, by contradiction, only r_{AVE} could have spawned χ_{MIN}. Further, and again by contradiction, only r_G can follow this r_{AVE} to assure that χ_{MIN} is preserved.

© 2003 NRC Canada

This final property effectively finishes our proof. We know that the temporal sequence of r_i values has a period, τ, by definition (each r_G is followed by $(\tau - 1)$ r_{AVE}s). Because the attractor has a global maximum corresponding to the following temporal sequence in r values $\{r_G, r_{AVE}\}$ and a global minimum corresponding to the temporal sequence $\{r_{AVE}, r_G\}$, then the period of the attractor must be either τ or $I\tau$, where I is any positive integer.

Further, one can prove that the τ-periodic solution always exists by starting with the following contrived initial value problem. Assume that all initial values correspond to χ_{MIN} and that $r_i = r_G$. During the first time unit, then, r_G invokes a spike in recruitment and we reach a local maximum before the sequence of $(\tau - 1)r_{AVE}$s cause the solution to strictly decrease (property *ii*). Upon some reflection, one sees that if the decrease goes beyond χ_{MIN}, then the dynamics suddenly fall into a perpetual cycle of decrease (with progressively lower local maximums associated with r_G). Similarly, if the decrease does not reach χ_{MIN}, then the next r_G invokes a spike in recruitment that must surpass the old local maximum and the solution finds itself spiraling ever upward. In both cases, either infinite increase or decrease, the resulting solution defies the fact that the solution is bounded. Therefore, the only possible periodic solution that results from this contrived initial value problem is the τ-periodic solution. Note, that this is not a proof of the local stability of this solution, only its existence.

Finally, we end by noting that this proof relies heavily on property *ii*; this property is violated for the overcompensatory case ($\gamma > 1$).

© 2003 NRC Canada

Quantifying migratory delay: a new application of survival analysis methods

Theodore Castro-Santos and Alex Haro

Abstract: Statistical techniques commonly used in fish passage research fail to adequately quantify delays incurred at obstacles, or the effects of modifications to those obstacles on passage rates. Analyses of telemetry data describing these effects can be misleading, particularly when passage route of some individuals is not established (e.g., because of mortality, tag failure, passage through unmonitored or alternate routes, etc.). Here, we demonstrate how event-time analysis, better known as survival analysis, can be used to quantify passage rates for any study that allows tracking of individuals through time, even when some individuals fail to pass the route or obstacle in question. We review two of the primary methods of event-time analysis (parametric and Cox's proportional hazards regression analyses) and use them in combination with logistic regression to provide unbiased estimates of delay incurred at a hydroelectric facility, as well as insights on factors affecting both rates of passage and route selection. Passage rate increased with increased depth of a surface bypass sluice gate and, among fish that passed through the turbines, with turbine flow. The data further indicate that risk of turbine passage increased with both delay and turbine flow.

Résumé : Les techniques statistiques couramment utilisées pour étudier le passage des poissons ne réussissent pas à quantifier adéquatement les délais face aux obstacles, ni à évaluer les effets des modifications de ces obstacles sur les taux de passage. Les analyses de données de télémétrie qui décrivent ces effets peuvent être faussées, particulièrement lorsque la voie de passage de certains individus ne peut être déterminée (e.g., à cause de la mortalité, de la perte des étiquettes, du passage par des routes non surveillées ou des routes de rechange, etc.). Nous démontrons comment l'analyse temporelle des événements (« event-time analysis »), mieux connue sous le nom d'analyse de survie, peut servir à quantifier les taux de passage dans toute étude qui permet de suivre des individus dans le temps, même lorsque certains ne suivent pas la route ou ne traversent pas les obstacles en question. Nous examinons deux des principales méthodes de l'analyse temporelle des événements (l'analyse de régression paramétrique et l'analyse de régression aléatoire proportionnelle de Cox) et les utilisons en combinaison avec la régression logistique pour obtenir des estimations non biaisées des délais encourus à un ouvrage hydroélectrique, de même que des informations sur les facteurs qui affectent à la fois les taux de passage et le choix de route. Les taux de passage augmentent en relation avec la profondeur d'une vanne de dérivation de surface et, chez les poissons qui passent par les turbines, en relation avec le débit de la turbine. Nos données montrent, de plus, que le risque associé au passage dans la turbine augmente tant avec le délai devant l'obstacle qu'avec le débit de la turbine.

[Traduit par la Rédaction]

Introduction

A growing body of research shows that delays to the migrations of anadromous fishes can cause dramatic reductions in adult recruitment and spawning success. For many species, the ability of juveniles to osmoregulate in both salt and fresh water (a prerequisite for successful transition to the marine environment) can only be maintained for a brief period (McCormick et al. 1998; Whalen et al. 1999). Similar time-dependent effects have been shown for thermal tolerance (Zydlewski and McCormick 1997*a*) and predation risk (Hargreaves 1994; Venditti et al. 2000). Failure of migrants to reach the marine environment within the resulting "smolt window" reduces likelihood of survival. Adult migrants are also vulnerable to delay: freshwater spawning migrations are often powered exclusively by energy stores acquired at sea, and growing evidence suggests there is a trade-off between depletion of these stores and reproductive success (Glebe and Leggett 1981; Leonard and McCormick 1999; Hinch and Bratty 2000).

Concern over the delays incurred at dams and similar barriers has caused the U.S. National Marine Fisheries Service (NMFS) to call for operational changes at hydroelectric facilities to minimize this effect (NMFS 2000). How the effects of these changes should be quantified, however, remains unclear. Migration rate is affected by numerous environmental variables including flow, temperature, photoperiod, and previous experience of the migrants (Zabel and Anderson 1997; McCormick et al. 1998). Although data from various forms of telemetry can provide detailed information on migratory behavior near obstacles, current analytical methods fail to make full use of incomplete data, i.e., data from indi-

Received 8 August 2003. Accepted 9 April 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 25 September 2003.
J17035

T. Castro-Santos[1] and A. Haro. United States Geological Survey, Biological Resources Division, Silvio O. Conte Anadromous Fish Research Center, One Migratory Way, P.O. Box 796, Turners Falls, MA 01376, U.S.A.

[1]Corresponding author (email: TCastro_Santos@usgs.gov).

 doi: 10.1139/F03-086 © 2003 NRC Canada

viduals that experience any form of tag failure, suffer predation, pass via undetermined routes, routes other than the route of interest, or fail to pass during the course of the study. Typically, such "censored" individuals are removed from the study and only those that pass are compared; alternatively, some analyses might require an assumption that the fish passed through one route or the other. Either approach introduces bias into the analysis and casts suspicion on the results (e.g., Nettles and Gloss 1987; Wilson et al. 1991; Johnson et al. 2000).

A further deficiency in standard analytical techniques is that they often fail to adequately account for covariates that change over time. Many variables that could potentially influence passage rate may not be constant during the prepassage period, and depending on delay duration, fish may be exposed to multiple levels of these covariates.

In this paper, we demonstrate how the problems of incomplete data, alternate passage routes, and time-varying covariates can be overcome using statistical methods best known for their applications in biomedical research. Collectively known as "survival analysis" (Cox and Oakes 1984; Lee 1992; Hosmer and Lemeshow 1999), these methods were developed to describe the timing of events, incorporating data from individuals that are removed from studies or whose fate was not determined before ending a study. Although the name implies application to survival studies, we use it here to quantify passage rate with no direct inference on survival. Thus, to avoid confusion with actual survival studies, we will use the synonym "event-time analysis".

Although these methods have broad application in ecological studies (e.g., Chambers and Leggett 1989) and have been used to estimate survival during the course of migration (Skalski et al. 1993; Lowther and Skalski 1997), they have yet to be applied to behavioral components of fish passage. Here, we present a novel application of event-time analysis and demonstrate its usefulness by quantifying effects of modifications at a hydroelectric facility on rates of passage. Results of a radiotelemetry study of migrating Atlantic salmon (*Salmo salar*) smolts were selected to demonstrate this application.

Methods

Rationale and techniques of event-time analysis

Because the theory and application of event-time analysis are unfamiliar to most fish passage researchers, we present a brief overview of event-time analysis techniques in the following subsections. Interested readers should consult Lee (1992), Allison (1995), and Hosmer and Lemeshow (1999) for more complete details. In each technique, a binary variable, δ, is used to denote whether the individual's passage time was observed ($\delta = 1$) or not (censored observations; $\delta = 0$). This allows calculation of probability functions without attributing passage routes or times to censored individuals. The only limitation to the use of censored data is that censoring must not be informative, i.e., covariate effects should be the same for censored and uncensored observations.

In addition to censoring, the feature that best distinguishes event-time analysis from other parametric and nonparametric methods is its use of the hazard and survivorship functions ($h(t)$ and $S(t)$, respectively). The hazard function is the instantaneous rate of passage for those individuals that have not yet passed, i.e.,

$$(1)\quad h(t) = \lim_{\Delta t \to 0} [P\{\text{an individual remaining at time } t \text{ passing in the interval } (t, t + \Delta t)\}/\Delta t]$$

The survivorship function is the complement of the cumulative distribution function and indicates the proportion of individuals remaining at time t.

$$(2)\quad S(t) = P\{\text{an individual passing after time } t\}$$

These relate to the more familiar probability density function (PDF, or $f(t)$)

$$(3)\quad f(t) = \lim_{\Delta t \to 0} [P\{\text{an individual passing in the interval } (t, t + \Delta t)\}/\Delta t]$$

in that $f(t) = h(t) \times S(t)$ (Lee 1992).

The utility of the hazard and survivorship functions becomes apparent when we consider the effects of censoring. Censored data preclude the usual approach of estimating mean and variance of passage times. The hazard function can be easily estimated, however, by dividing numbers of fish passing in an interval by the number of fish available to pass. Likewise, because censoring indicates that the fish has not yet passed, the last extant observation still contributes to the calculation of the survivorship function (see below).

The most straightforward approach to describing passage times and their associated probability functions is to construct a life table. This is done by breaking time down into meaningful, but not necessarily equal, intervals and calculating estimates of the above probability functions. Lee (1992) provides a clear and detailed description of this procedure. An alternative approach, developed by Kaplan and Meier (1958), is helpful when plotting data. Here, instead of being fixed, intervals are defined by the actual occurrence of events. At each time that a passage event occurs, the value of the survivorship function is estimated based on the cumulative product of the conditional proportion passing:

$$(4)\quad \hat{S}'(t) = \prod_{i:t_i \le t} \left[1 - \left(\frac{p_i}{n_i}\right)\right]$$

where p_i of n_i available individuals pass at each time t_i. Note that the t_i's refer only to uncensored observations, but both censored and complete observations are included in the denominator (n_i, or the risk set) as long as they remain available to pass. Life-table methods are best for constructing tables, Kaplan–Meier curves are best for plotting data. Nonparametric tests and predictions can be generated based on either life-table or Kaplan–Meier methods with similar results. However, when multiple covariate effects are present, these tests may be inappropriate, so we avoid them here.

Parametric models for event-time data with censoring

The influence of covariates on passage rate, as well as the shape of probability functions, can often be described by fitting models to the data and testing for fit. Covariate effects can be readily expressed as a linear model. An intuitive form is the accelerated failure time (AFT) model (Allison 1995; Hosmer and Lemeshow 1999):

© 2003 NRC Canada

$$(5) \qquad \ln(T) = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k + \varepsilon$$

where passage time T is a random variable conditional on covariates $x_{1,\ldots,k}$. The disturbance component ε determines the shape of the error distribution and thus the spread of the quantile estimates of passage time. Note that the "failure" term in AFT carries over from the survival analysis literature but refers here to passage events. Using this approach, covariate effects are multiplicative: a given quantile of passage time T changes by a factor of e^{β_j}, or increases by $100(e^{\beta_j} - 1)$ percent per unit increase in the covariate.

Most texts and computer programs fit these models using maximum likelihood (ML) estimation (Lee 1992). The likelihood, L, of a model is described by

$$(6) \qquad L = \prod_{i=1}^{n} [f_i(t_i)]^{\delta_i} [S_i(t_i)]^{1-\delta_i}$$

where $f_i(t_i)$ and $S_i(t_i)$ are, respectively, the estimated PDF and survivorship functions of the fitted distribution for each individual, contingent on model covariates, and $\delta_i = 0$ for censored and 1 for uncensored observations. The likelihood function is maximized with respect to model covariates and parameters, usually by applying some version of the Newton–Raphson algorithm (Lee 1992).

The presence of censored data complicates the evaluation of model fit. Although Allison (1995) and Hosmer and Lemeshow (1999) provide a method for calculating a generalized R^2 statistic, both texts caution against its use, because its value is affected by the proportion of censored observations in the data set; indeed, no statistic can be calculated that quantifies the proportion of variance in a data set that is accounted for by a given model, because the variance of censored observations is not known. Therefore, alternative methods must be used for evaluating model fit. The log-likelihoods of ML-generated models can be used to test for differences in fit between nested distributions and models: a significant likelihood ratio indicates superior fit of the model with the greater likelihood. Akaike's information criterion (AIC) can also be used to identify the best distribution or model and has the advantage of not requiring nesting (see Allison (1995) for a clear discussion of nested distributions and Burnham and Anderson (1998) for the theory and application of AIC).

A more general method for numerically testing whether the data follow a particular distribution was proposed by Hollander and Proschan (1979), summarized in Lee (1992): a statistic following the standard normal distribution is calculated by comparing predicted and observed values of the survivorship function. In a related approach, Cox–Snell residuals (defined as $e_i = -\ln(S(t_i|\boldsymbol{x}_i))$, where $\boldsymbol{x}_i$ is the vector of covariate values for individual i and $S(t_i)$ is the estimated probability of that individual remaining until time t, based on the fitted model) are plotted against $-\ln(S'(t_i))$, where $S'(t_i)$ is the Kaplan–Meier estimate of the survivorship function. If the model adequately describes the data, then this plot yields a straight line with a slope of unity (Allison 1995).

Cox's proportional hazards regression

More often than not, knowledge of underlying distributions is limited, or the complexity of the shape of those distributions precludes predictive modeling. Furthermore, the presence of covariates that change over time can complicate modeling efforts and may not even be possible using many standard software packages. The effect of various treatments on the hazard function can still be estimated, however, using a semiparametric, proportional hazards regression approach first described by Cox (1972). This model is based on the premise that the log of the hazard is a linear function of k covariates; the relationship between the hazard functions of two treatment groups i and j is described by

$$(7) \qquad \ln(h_i(t) - h_j(t)) = \beta_1(x_{i1} - x_{j1}) + \beta_2(x_{i2} - x_{j2}) + \ldots + \beta_k(x_{ik} - x_{jk})$$

The effects of covariates on the ratio of the two hazards are estimated by the coefficients $\beta_1, \ldots, \beta_k$. This approach is similar to that described above for the parametric regression model, with the important distinction that where the parametric regression uses ML to model the effects of covariates on the actual time of the event, Cox's proportional hazards regression uses partial likelihood (L_P) to describe their effects on the rate at which the event occurs. A general expression for the L_P of a proportional hazards model with fixed (i.e., not time-varying) covariates is

$$(8) \qquad L_P = \prod_{i=1}^{n} \left[\frac{e^{\boldsymbol{x}_i \boldsymbol{\beta}}}{\sum_{j \in R(t_i)} e^{\boldsymbol{x}_j \boldsymbol{\beta}}} \right]^{\delta_i}$$

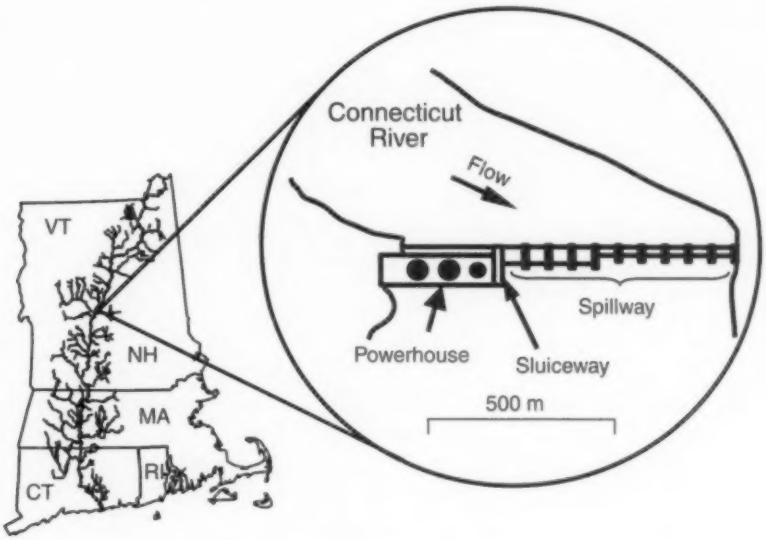
where $R(t_i)$ constitutes the risk set, all individuals available to pass at time t_i (equivalent to n_i in eq. 4) and $\boldsymbol{x}\boldsymbol{\beta}$ refers to the vector product of the covariates and their coefficients, either for the individual passing (i) or for each member of the risk set (j). As with ML estimation, the L_P is then maximized with respect to $\boldsymbol{\beta}$ using the Newton–Raphson algorithm. Note that by constructing the denominator in this way and including the censoring indicator δ_i, censored data are included in the analysis and contribute to the denominator until the last extant observation.

Because the L_P is based on the rank of time, rather than its actual value, combined, relative covariate effects on the hazard function can be tested without requiring the underlying probability to follow a particular distribution. In addition to significance, software packages may generate estimates of coefficients in eq. 7; their interpretation is simplified by using an alternate quantity, the hazard ratio, which equals e^{β_j} and indicates the proportional change in hazard per unit change in the covariate.

Another attractive feature of proportional hazards regression is that because it makes no assumptions about the underlying hazard function, inclusion of covariates that change over time is a simple process that is included as a standard feature in many software packages. Hazards are calculated at each event time based on the current risk set, regardless of whether individuals had previously been exposed to a different set of covariate values.

© 2003 NRC Canada

Fig. 1. Plan view of Wilder Station (42°40′N, 72°18′W) showing location of forebay, powerhouse, and sluiceway. Inset shows location of facility on the Connecticut River in northeastern U.S.A. (VT, Vermont; NH, New Hampshire; MA, Massachusetts; CT, Connecticut; RI, Rhode Island).



Although Cox's proportional hazards regression is not fully parametric, it still requires certain assumptions about the data, primarily that the effects of covariates on hazard are constant over time. Deviation from this assumption can cause misleading results. The proportional hazards assumption can be tested by plotting Shoenfeld residuals (Shoenfeld 1982; Grampsch and Therneau 1994) against the log of time (any significant slope indicates that proportionality is time-dependent). Another residual, called the score residual, is useful for identifying influential and poorly fit observations (see Hosmer and Lemeshow (1999) for a thorough discussion of fit evaluation for proportional hazards models).

Competing risks

The binary approach to censoring applied in the preceding sections is complicated by the availability of multiple passage routes, a common feature of downstream passage studies. Before passage, fish are available to pass through all routes, i.e., they are part of the risk set. Once a route is selected, however, they no longer contribute to the passage rate of any route. In other words, an individual passing via a given route is effectively censored with respect to the other routes. This constitutes a competing risks situation for which event-time analysis methods are particularly well suited (Allison 1995).

When confronted with a competing risks situation, a multistep approach is appropriate. First, all covariates except passage route are included in the model. This allows inclusion of individuals that were not observed passing through either route (i.e., censored observations) and provides the best estimate of overall passage rate. Next, separate models are developed for individuals passing through each route of interest by modifying the censoring variable. For each model, non-passers, as well as those that pass through alternate routes, are included, censored at time of passage; only those that pass through the route of interest are noncensored. The advantage of this step is that it evaluates separately variables that affect the rates at which fish pass through each route. Although different results for competing passage routes suggest some underlying difference in covariate effects on passage rate that may be of substantial biological interest, the competing risks approach does not test for these differences explicitly; it is simply a means of quantifying covariate effects on passage rates through a particular route. This means that researchers can use the entire risk set when analyzing passage rates through any route, or combination of routes, and the approach can be applied to any of the methods detailed above, a potent tool for evaluating the effects of facility operations on passage rate through a particular route. The only assumption required is that fish that have not yet passed the dam are equally available to pass via all routes and should be included when evaluating the effects of covariates on the groups.

Logistic regression

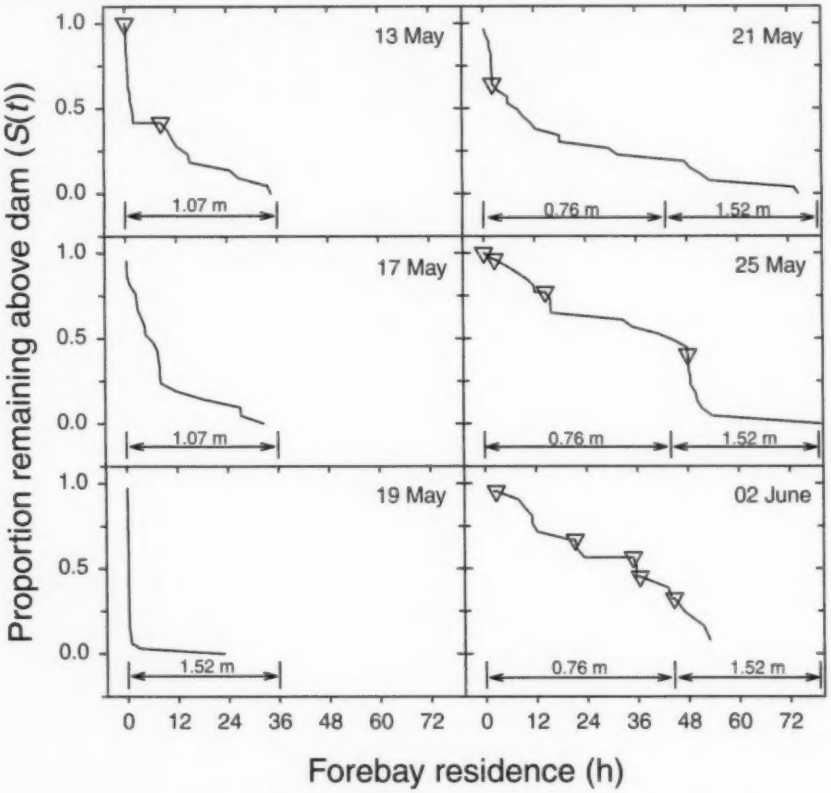
Although the competing risks approach allows separate analysis of rates of passage through various routes, it does not directly quantify which variables most influence the likelihood of selecting one route over another. Logistic regression is a standard method for quantifying covariate effects on the likelihood of selecting one of two or more categorical variables (Hosmer and Lemeshow 1989). By including time as a covariate, the effect of delay on passage route selection can be tested directly. Censored individuals, because they are not observed to actually pass, are generally not included in such analyses (Allison 1995).

Data set

We selected a sample data set (RMC Environmental Services, Inc., currently Normandeau Associates, 917 Route 12,

© 2003 NRC Canada

Fig. 2. Kaplan–Meier curves describing forebay residence times of radio-tagged Atlantic salmon (*Salmo salar*) smolts passing Wilder Station during each of six releases. Open triangles indicate censored individuals. Gate depth is indicated in each panel, as well as shifts from 0.76 m to 1.52 m during the last three releases. Note the rapid passage on the 19 May release and increased passage rate following increased gate depth during the last three releases.



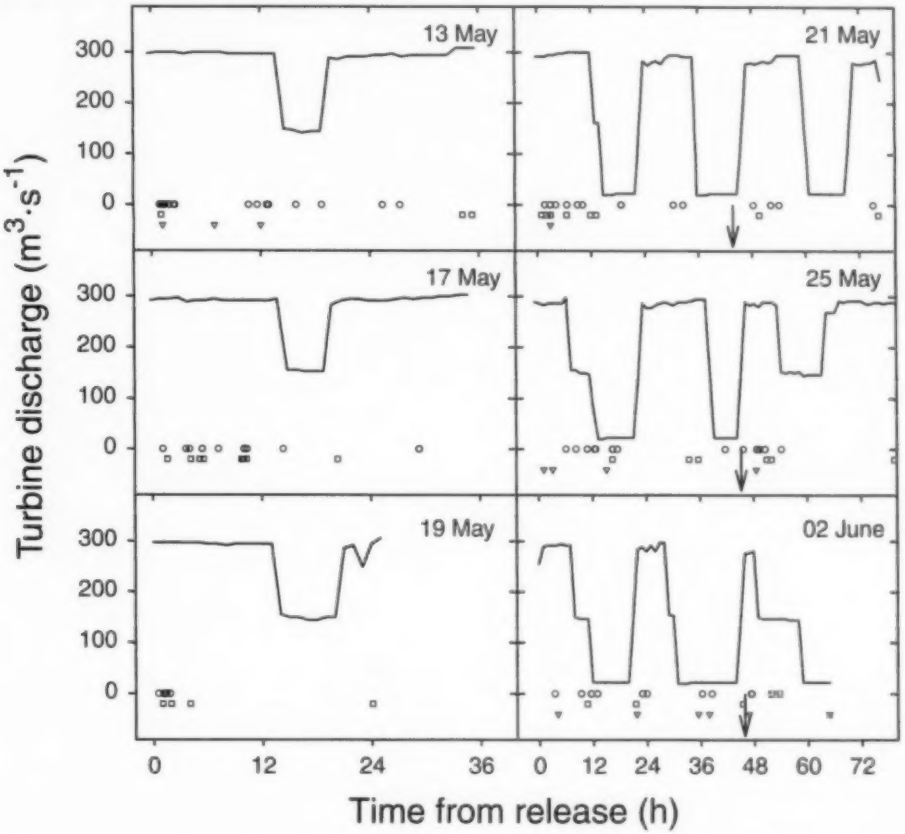
Suite 1, Westmoreland, NH 03467, U.S.A., unpublished data) to demonstrate the utility of each of the event-time analysis methods for describing the effects of operational modifications and other variables on delay. Here we define delay as the time elapsed between forebay entry and passage, i.e., forebay residence time. The study was conducted in 1994 at Wilder Station, a hydroelectric facility on the Connecticut River mainstem at river-kilometre 348, and was designed to test the effect of different depth settings of a bypass sluice gate on passage route selection. The ice–log sluice used for downstream smolt passage is located adjacent to the powerhouse (Fig. 1). A 3.0 m × 4.6 m skimmer gate regulates surface flows of 1.38 $m^3 \cdot s^{-1}$ at 0.305-m depth to 18.7 $m^3 \cdot s^{-1}$ at 1.83-m depth. When operated for smolt passage, the gate is normally set to 1.07-m depth, passing 8.77 $m^3 \cdot s^{-1}$ down an 18.3-m-long sluice into the station tailrace. The powerhouse contains two 19-MW Kaplan turbines and one 3.2-MW generator, protected by trashracks with 15 cm horizontal and 48 cm vertical spacing. No spill occurred during this study, so all flow passed through the turbines or over the bypass sluice. These were the only two passage routes available to the smolts during this period.

Atlantic salmon smolts were obtained from two sources: a bypass sampler on the Connecticut River mainstem ("wild" fish; n = 65, fork length (FL) = 137–235 mm, $\overline{FL}$ = 179 mm), and the White River National Fish Hatchery in Bethel, Vermont ("hatchery" fish; n = 93, FL = 152–218 mm, $\overline{FL}$ = 190 mm). Source of fish is referred to as "origin" and coded 0 and 1, respectively, for wild and hatchery smolts in analyses. Smolts were anaesthetized using MS-222 and radio-tagged using esophageal implants. Following a 24-h recovery period, fish were released 1 km upstream of Wilder Station. This was considered sufficient distance to prevent any predisposition on the part of the smolts to pass through one route over the other. Smolts were released in six groups of 21–33 individuals on 13, 17, 19, 21, and 25 May and 2 June 1994 (Fig. 2). Wild fish made up 48% (33–58%) of the first five releases; the last release consisted of hatchery fish only. Telemetry receivers were placed in such a way that smolts were detected when they entered the forebay of the project (which extended about 200 m upstream of the dam) and were monitored continuously during their forebay residence. A four-element YAGI antenna situated halfway down the sluice identified sluice passers, and antennas submerged at the entrance of each intake identified turbine passers. Time to passage (delay or residence time) was calculated from the time that fish first entered the forebay to ensure that only data from actively migrating fish were used.

Turbine flow was logged each hour and ranged from 19.8 to 308 $m^3 \cdot s^{-1}$, $\overline{X}$ = 253 $m^3 \cdot s^{-1}$. Because fish that did not im-

© 2003 NRC Canada

Fig. 3. Turbine flow at Wilder Station during each of six releases. Data are presented as hours from each release. Points indicate passage time for sluice passers (circles) and turbine passers (squares); censored times are indicated by triangles. Arrows indicate time to increased gate depth in each of the last three releases.



mediately pass the station were often subjected to more than one level of turbine flow (Fig. 3), this was not included in the parametric models but was included as a time-dependent covariate in the proportional hazards models.

A similar complication arose with respect to sluice gate depth. This was set to 1.07 m for the first two releases, 1.52 m for the third release, and 0.76 m for the last three releases. For each of the last three releases, the sluice gate depth was increased to 1.52 m after 44–46 h (Fig. 2). To prevent the artificial association of greater gate depth with long passage delays, we censored data from these releases at the corresponding residence times for the parametric regression analysis but included the data with gate depth as a time-dependent covariate in the proportional hazards analysis.

Because fish could only pass through the turbines or over the sluice, passage route constituted a competing risks variable in this study. Separate models were generated for each route as well as for the combined data using fully parametric and Cox's proportional hazards techniques. To test for differences between routes in covariate effects on passage rate, we ran the above tests, including route and its interactions with the other covariates.

We used SAS software (SAS 1999) to estimate covariate effects on passage time. We selected from among exponential, Weibull, lognormal, and generalized gamma distributions, testing for the best fit using likelihood ratio statistics and AIC. Where nested models were not significantly different from each other, we selected the most parsimonious model, i.e., the one with the fewest parameters. Adequacy of the parametric models was evaluated both numerically and graphically, using each of the methods detailed above. We evaluated adequacy of proportional hazards models using Schoenfeld and score residuals.

In addition to the above tests, we used logistic regression to test for covariate effects on likelihood of passing through the bypass sluice, including log of delay time as a covariate. All analyses were conducted using SAS software (SAS 1999).

Results

Of the 158 Atlantic salmon smolts used in this study, 14 (eight hatchery and six wild) had undetermined passage routes or failed to pass; these were included in the analyses, censored at their last extant observation. In all, 144 smolts passed the station by known routes: 106 over the bypass sluice and 38 through the turbines. Most fish entered the forebay shortly after release; mean ± standard deviation (SD) of postrelease delay was 1.27 ± 1.70 h, with all but three in-

© 2003 NRC Canada

Table 1. Results from parametric and Cox's proportional hazards regression.

		Parametric			Proportional hazards		
Data set	Variables	N	$\hat{\beta}$	P value	N	$\hat{\beta}$	P value
Combined data	Number passed	121			144		
	Number censored	37			14		
	Intercept		–787.190	0.018		—	—
	Origin		–0.007	0.981		0.042	0.810
	Release date		0.063	0.017		–0.019	0.323
	Turbine flow ($m^3 \cdot s^{-1}$)		—	—		0.001	0.611
	Gate depth (m)		–5.459	<0.001		3.528	<0.001
	Scale		1.589			—	—
Sluice passers	Number passed	89			106		
	Number censored	69			52		
	Intercept		–499.125	0.183		—	—
	Origin		0.163	0.609		–0.055	0.787
	Release date		0.040	0.175		–0.025	0.289
	Turbine flow ($m^3 \cdot s^{-1}$)		—	—		–0.003	0.210
	Gate depth (m)		–6.316	<0.001		3.972	<0.001
	Scale		1.695			—	—
Turbine passers	Number passed	32			38		
	Number censored	126			120		
	Intercept		–1460.460	0.034		—	—
	Origin		–0.462	0.406		0.316	0.378
	Release date		0.117	0.033		–0.029	0.433
	Turbine flow ($m^3 \cdot s^{-1}$)		—	—		0.009	0.024
	Gate depth (m)		–2.562	0.039		1.820	0.068
	Scale		2.185			—	—

Note: The competing risks approach was applied to each passage route, where censored individuals include those passing through the alternate route. Parametric models are based on the lognormal distribution: coefficients (β) indicate effect of each variable on the log of delay ($\ln(T)$); scale refers to the error term. Coefficients for the proportional hazards models indicate their effect on the log of the hazard ($\ln(h(t))$). Origin is coded 1 (hatchery) and 0 (wild).

dividuals entering within 4 h. Kaplan–Meier survivorship curves of residence time ($S'(t)$; Kaplan and Meier 1958) are presented for each release group (Fig. 2).

Results from both parametric and proportional hazards models (Table 1) should be interpreted with some caution, as there was significant collinearity among covariates. This effect was greatest between release date and both gate depth and turbine flow. Correlation coefficients were in all cases less than 0.45, however, and the effect of collinearity on the models should be small.

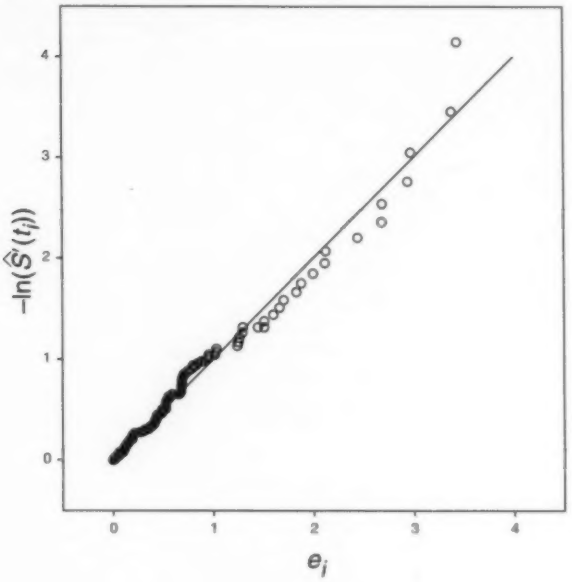
Among the parametric models, the generalized gamma distribution provided a better fit to the combined data than did the Weibull or exponential distributions (χ^2; 1 and 2 df, respectively; $P < 0.001$). However, the lognormal and gamma distributions provided nearly identical fits (χ^2; 1 df; $P = 0.81$). Based on these results, combined with the AIC values, the Hollander and Proschan test ($P = 0.20$), and analysis of Cox–Snell residuals (Fig. 4), we concluded that the lognormal distribution was the most appropriate and parsimonious of the distributions tested and that it adequately described the data. Under this parameterization, the scale variable is analogous to the error term under the standard normal distribution; location is estimated by $\mathbf{x}\boldsymbol{\beta}$. The estimated scale values of 1.6–2.2 indicate that passage rate (i.e., hazard) follows an inverted U shape: initially low, it rapidly increases to a maximum value and then declines gradually over time (Meeker and Escobar 1998).

Coefficients of the parametric models indicate covariate effects on $\ln(T)$. These describe reduced delay with increased gate depth for combined passage data and for both passage routes, as indicated by a significant negative coefficient. The interpretation of this for the combined data, adjusting to centimetres, is $T = 100(e^{-0.055} - 1)$, or mean delay decreases by 5.4% for every centimetre of increased gate depth. The same transformation for sluice and turbine passers shows a 6.1% and 2.6% decrease in delay time per centimetre increase of gate depth, respectively. For the current data set, this implies that by increasing gate depth from the shallowest to deepest settings and setting all other covariates to their mean values, median delay declines from 19.9 to 0.3 h when both passage routes are available, and delay of the 90th percentile declines from 152.8 to 2.4 h (Table 2). The parametric approach also suggests that fish released later in the study passed more slowly than earlier releases (positive β), regardless of passage route.

Results of proportional hazards regression indicate that gate depth affected passage rate, particularly among sluice passers (Table 1). Faster passage rate at greater depths is indicated by a significant positive coefficient (greater hazard; note the contrast with the parametric approach). Adjusting to centimetres and transforming the data to risk ratios, we find here a 3.6% increase in passage rate associated with each centimetre of gate depth for combined data and a 4.0% increase for sluice passers.

© 2003 NRC Canada

Fig. 4. Graphical assessment for goodness-of-fit of the lognormal parametric regression model using the total data set (sluice and turbine passers combined). Cox–Snell residuals (e_j) are plotted against the negative log survivorship function ($-\ln(\hat{S}'(t))$), calculated using the Kaplan–Meier method (circles). A line with slope of unity, an indicator that the model provides a reasonable fit, has been included for reference.



Turbine flow also affected passage rate, but only among fish that passed through the turbines. Here, the positive coefficient indicates a hazard ratio of 1.009. Over the range of turbine flows encountered in this study, this means that the rate of fish passage through the turbines was 2.6 times greater under the highest flow than under the lowest flow.

Residual analysis confirmed that the assumption of proportionality was met in these models. However, analysis of the score residuals suggested that the last fish to pass from the 19 May release was influencing the results, particularly with respect to the coefficients for gate depth. When this individual was removed from the analysis, the coefficients for total data and sluice passers increased to 4.7% and 5.3% per centimetre increase in gate depth, respectively. The only other notable effect of removing this data point was to increase the P value for the coefficient describing the gate depth effect on turbine passers to 0.121, casting further doubt on its importance.

Significance tests for different effects of gate depth and turbine flow on rates of sluice and turbine passage suggested that covariate effects did differ between the two routes, although neither the parametric nor the proportional hazards approach found a significant difference in passage rate by route (main effect), the interaction of route × gate depth was strongly significant for both models ($P < 0.001$). In contrast, the interaction of route × turbine flow was only marginally significant ($P = 0.063$; proportional hazards model only). It is important to emphasize here that these tests, because they include passage route, exclude the censored observations and should therefore be considered biased approximations.

Table 2. Predicted delay times from the parametric regression model (Table 1) for median and first and last deciles of Atlantic salmon smolts passing a hydroelectric facility by either route ("combined data") under three different sluice gate settings.

			95% bounds	
Gate depth	Percent passed	Predicted delay (h)	Lower	Upper
0.76	10	2.60	1.83	3.71
	50	19.94	14.56	27.32
	90	152.78	101.16	230.77
1.07	10	0.49	0.37	0.66
	50	3.78	3.02	4.73
	90	28.93	20.67	40.50
1.52	10	0.04	0.02	0.07
	50	0.31	0.19	0.50
	90	2.38	1.41	4.03

Table 3. Logistic regression results describing the effect of covariates on passage route selection.

Source	$\hat{\beta}$	P value
Intercept	–4.0930	0.9936
Origin	–0.3732	0.3931
Release date	0.0004	0.9904
Turbine flow ($m^3 \cdot s^{-1}$)	–0.0077	0.0158
Gate depth (m)	0.4549	0.0339
ln(hours)	–0.2651	0.0234
N	144	

Note: Positive coefficients ($\hat{\beta}$) mean increased probability of sluice passage; origin was denoted as 1 (hatchery) and 0 (wild); gate depth and turbine flow indicate settings at time of passage. Fish that failed to pass were excluded from this analysis; sample size (N) refers to passers only.

The logistic model (Table 3) demonstrates that the probability of turbine passage increases with delay (note that data from censored individuals are omitted). Probability of turbine passage was likewise increased by greater turbine flow but was reduced by greater sluice gate depth.

Discussion

Although the results of this study inevitably have management implications, readers should bear in mind that our objective is to introduce a new technique and demonstrate its use. RMC (1994) correctly concluded that the gate depth setting of 1.52 m afforded more expedient downstream passage to emigrating smolts and the sluice is currently operated at this depth for fish passage. Therefore, the intent of this paper is not to call into question existing management decisions, but to present techniques that will lead to further and more complete investigations of bypass configurations and other passage evaluations. Moreover, it is important to recognize that although we define delay here as forebay residence time, the term implies a change relative to some minimum transit time. This value is unknown, but its identification and characterization should be an objective of future studies.

© 2003 NRC Canada

Our results do highlight some important differences among the event-time analysis techniques, as well as their relative strengths. Survivorship curves are simple to construct, and their significance is readily interpreted. Here, they show that although the first half of the fish pass fairly quickly, passage rate declines with time and the slowest fish take several days to pass the project. Reporting only median passage time masks this important feature (Venditti et al. 2000), a fact that should be of some concern to restoration efforts. The survivorship curves also provide graphical representation of the effects of sluice gate depth setting. Delay times were least for the 19 May release (gate depth of 1.52 m) and greatest for the last three releases (gate depth of 0.76 m). Those fish that delayed passage until after the gate was set to a greater depth show a correspondingly greater rate of passage at that time.

More censoring was observed for later release dates and shallower gate settings. However, there is no reason to believe that censored and complete observations differed with respect to their response to covariate values. With the exception of the competing risks models, the exact cause of censoring was not determined and may have been due to mortality, tag failure or expulsion, or undetected passage.

Although nonparametric methods for analyzing data with censored observations exist, adequate sample size and the presence of multiple, nonorthogonal covariates indicated the use of a regression approach in this analysis. Both the parametric and Cox's proportional hazard models simultaneously account for all covariate effects (Type III hypotheses; SAS 1999), but they differ in important ways. First, because the parametric models describe covariate effects on forebay residence time, we are able to use them to estimate time to passage of specific proportions of the population at defined covariate levels, a useful tool for managers and those interested in understanding population-level implications of delay. The proportional hazards models, by contrast, describe covariate effects on passage rate (hence the reversed sign of the regression coefficients: passage rate is inversely related to residence time) and cannot be used to directly estimate delay time (but see Hosmer and Lemeshow (1999) for methods by which indirect estimates can be extrapolated).

The parametric models can also be used to draw important inferences on the shape of the hazard and consequently the distribution of quantiles. Here, the numerical and graphical goodness-of-fit analyses both suggest that the lognormal models provide a reasonable fit to the data. This implies that the log delay times are approximately normally distributed (Allison 1995). The inverted U-shaped hazard function described by these models may have some biological significance, as it implies both initial delay (as might be expected from time required to locate the passage route) and reduced passage rates for fish that do not subsequently pass quickly. Thus, the risks of delay include increased likelihood of further delay, a pattern that one would predict if delay resulted in loss of migratory motivation (Meeker and Escobar 1998).

Although the Cox's proportional hazards models do not yield parametric descriptions of the hazard, their independence from specific distributions make them robust against fluctuating passage rate, e.g., resulting from diel migratory patterns, requiring only that covariate effects on hazard ratios be consistent across these patterns. With either approach, we advise against extrapolating far beyond observed values of covariates or delay times.

A further distinction is that proportional hazards models allow ready computation of effects of covariates that change over time, whereas the parametric models assume that each fish is exposed to fixed covariate conditions. This feature has important implications for the interpretation of the effects of release date and gate depth, as well as turbine flow. Because the shallowest gate settings were applied at the end of the experiment, the experimental design was unbalanced, and variability caused by this factor is wrongly apportioned between gate depth and release date under the fully parametric model. By including gate depth as a time-dependent covariate, potentially confounding effects between the two variables are reduced. Under this less biased interpretation of the data, delay is appropriately attributed to gate depth and not to date.

Similarly, fluctuations in turbine flow precluded its inclusion in parametric models — any quantity used (e.g., initial, mean, or final turbine flow) would yield misleading results, because it would not reflect the range of flows to which individual fish were exposed with their associated passage rates. As with the sluice gate settings, minimum daily discharge was less for later releases, and the significant date factor in the parametric models may have arisen in part from the covariance between date and discharge. When turbine flow was included in the proportional hazards models as a time-dependent covariate, it was found to significantly increase the rate of turbine passage, but not sluice passage, and was nonsignificant for the total data.

Both turbine passage models, with their weak effects of turbine flow and gate depth, also illustrate one of the limitations of event-time analysis: because only 38 fish passed through the turbines, over 75% of the observations are censored. This increases the standard error of the estimates, and the power of these models decreases with increased censoring. Thus, the weak significance values for gate depth should be viewed with caution: it may be that increased gate depth does increase passage rate for fish that pass through the turbines (as indicated by the parametric model), but the proportional hazards model lacked sufficient power to detect this effect.

The competing risks condition of this study illustrates the utility of event-time analysis techniques in analyzing passage data. The experimental design reasonably allows one to ask the question: does gate depth affect the passage rate through the bypass sluice? Including turbine passers among the censored data provides the clearest, least-biased answer to this question. Conversely, by censoring sluice passers, we were able to detect the effect of turbine flow on rate of passage through the turbines, which was not apparent from the analysis of the total data. This approach, however, does not directly test for the significance of differences in passage time between the two routes. Indeed, in the presence of censored data, there is no available way to conduct such a test objectively. Here, we constructed a model on the noncensored data that included passage route and the interactions of route × gate and route × turbine flow. The results showed strong significance for the former test but marginal significance for the latter. Because data from censored fish are omitted, these results are of necessity biased; at best, the

© 2003 NRC Canada

resulting models tend to underestimate time to passage (eq. 6). They do, however, describe the data from those fish with observed passage times and routes and further support the results of the competing risks analysis.

Whether the increased passage rate with increased gate depth resulted directly from the associated increase in flow or whether it reflects behavioral avoidance of the surface is unclear from this study. Surprisingly, greater gate depth was also associated with increased turbine passage rate. This may be because increased flow over the sluice attracted fish to the powerhouse area or otherwise altered forebay hydraulics such that fish passed more quickly through both routes. The effect of turbine flow supports the view that hydraulics affect passage rate, but the results for sluice passers remain ambiguous. Future studies should attempt to simultaneously control for volume and depth of bypass flows, as well as the ratio of bypass flow to turbine flow, to improve orthogonality of these factors.

Each of the techniques described above has specific advantages and can provide unique information on passage rate. The most appropriate approach will depend on time resolution (Cox's proportional hazards regression can incorporate ordinal time data, whereas parametric regression requires a continuous time variable), shape of the hazard function, and research objectives. None of the above techniques, however, quantifies covariate effects on route selection as such. Logistic regression does just this and thereby complements event-time analysis. Bearing in mind that data from 14 individuals are missing, logistic regression reveals a significant time effect, with greater delays associated with increased risk of turbine passage. This result alone can be a powerful argument for trying to maximize passage rates. Also significant in the logistic model are effects of turbine flow and gate depth, with greater flow and shallower gate settings associated with increased risk of turbine passage.

Combining the logistic and event-time approach, we conclude that shallower gate depth not only increased delay, but also simultaneously (in part, because of the delay) increased the likelihood of turbine passage, particularly in the presence of high turbine flows. These results illustrate the complementary nature of event-time and logistic regression approaches: shallower sluice gate settings reduced passage rates, especially through the sluice. This, in turn, increased the time during which fish were exposed to the possibility of passing through both routes, thereby increasing the likelihood of turbine passage. Thus, by modifying operations to maximize the rate at which fish pass over the sluice, both delay and likelihood of turbine passage could be minimized simultaneously.

The bulk of current fish passage research work focuses on proportions of fish passing through various routes, primarily because this is thought to have the greatest relevance to survival and recruitment (Burnham et al. 1987; Skalski 1998; Skalski et al. 1998). Although the importance of delays to migration is not well understood, it is bound to vary by species, river system, and life history (McCormick et al. 1996; Zydlewski and McCormick 1997*b*; Zabel et al. 1998). Our understanding of the effect of delay is limited at the outset by our ability to quantify it. Event-time analysis provides a powerful set of tools for developing just such descriptions, as well as for evaluating effects of structural and operational modifications on passage rates. Because they afford continuous monitoring of individuals, radiotelemetry and acoustic telemetry are particularly well suited to these analyses. Other forms of telemetry and monitoring (e.g., from passive integrated transponder (PIT) tags) may also be useful; however, it is important that time to passage or censoring is known. Because PIT tags tend to have relatively short read ranges (Prentice et al. 1990; Castro-Santos et al. 1996), it may not always be possible to identify censoring times using this technology, although the competing risks approach could still be applied to some data.

Although this paper focuses on the application of event-time analysis to a radiotelemetry study of downstream fish passage, the techniques have much broader potential. Analogous applications include quantifying attraction of upstream migrants to fishway entrances, monitoring progress up fishways (where height can be substituted for time as the dependent variable and successfully exiting the top of the fishway constitutes censoring), and quantifying timing of movements of other migratory species: in short, any application may be appropriate where censoring and competing risks confound the use of standard techniques.

Acknowledgments

The following individuals provided valuable assistance in the preparation of this report: James F. Jekel (Yale University, School of Public Health) provided early insight into the relevance of event-time analysis techniques to fish passage applications and Michael Sutherland (University of Massachusetts Statistical Consulting Services) and Paul Allison (University of Pennsylvania Sociology Department) provided guidance and instruction on event-time analysis techniques. We are particularly grateful to Timothy Brush and Brian Hanson (Normandeau Associates, Westmoreland, N.H., formerly RMC Environmental Services) for providing the data set (courtesy of New England Power Company, now PG&E National Energy Group, Concord, N.H.), as well as extensive support and comments on the manuscript. David Hosmer and two anonymous reviewers provided careful reviews and many helpful recommendations for the final draft.

References

Allison, P.D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute Inc., Cary, N.C.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference. A practical information-theoretic approach. Springer-Verlag New York Inc., New York.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., and Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, Md.

Castro-Santos, T., Haro, A., and Walk, S. 1996. A passive integrated transponder (PIT) tagging system for monitoring fishways. Fish. Res. **28**: 253–261.

Chambers, R.C., and Leggett, W.C. 1989. Event analysis applied to timing in marine fish ontogeny. Can. J. Fish. Aquat. Sci. **46**: 1633–1641.

Cox, D.R. 1972. Regression models and life tables. J. R. Statist. Soc. **34**: 187–220.

Cox, D.R., and Oakes, D. 1984. Analysis of survival data. Chapman and Hall, New York.

© 2003 NRC Canada

Glebe, B.D., and Leggett, W.C. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. Can. J. Fish. Aquat. Sci. **38**: 806–820.

Grampsch, P.M., and Therneau, T.M. 1994. Proportional hazards tests in diagnostics based on weighted residuals. Biometrika, **81**: 515–526.

Hargreaves, N.B. 1994. Processes controlling behaviour and mortality of salmonids during the early sea life period in the ocean. Nord. J. Freshw. Res. **69**: 97.

Hinch, S.G., and Bratty, J. 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. Trans. Am. Fish. Soc. **129**: 598–606.

Hollander, M., and Proschan, F. 1979. Testing to determine the underlying distribution using randomly censored data. Biometrics, **35**: 393–401.

Hosmer, D.W., and Lemeshow, S. 1989. Applied logistic regression. John Wiley and Sons, Inc., New York.

Hosmer, D.W., and Lemeshow, S. 1999. Applied survival analysis. John Wiley and Sons, Inc., New York.

Johnson, G.E., Adams, N.S., Johnson, R.L., Rondorf, D.W., Dauble, D.D., and Barila, T.Y. 2000. Evaluation of the prototype surface bypass for salmonid smolts in spring 1996 and 1997 at Lower Granite Dam on the Snake River, Washington. Trans. Am. Fish. Soc. **129**: 381–397.

Kaplan, E.L., and Meier, P. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. **53**: 457–481.

Lee, E.T. 1992. Statistical methods for survival data analysis. John Wiley & Sons, New York.

Leonard, J.B.K., and McCormick, S.D. 1999. Effects of migration distance on whole-body and tissue-specific energy use in American shad (*Alosa sapidissima*). Can. J. Fish. Aquat. Sci. **56**: 1159–1171.

Lowther, A.B., and Skalski, J. 1997. The design and anlysis of salmonid tagging studies in the Columbia Basin. Vol. VII. A new model for estimating survival probabilities and residualization from a release–recapture study of fall chinook salmon (*Oncorhynchus tshawytscha*) smolts in the Snake River. U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg.

McCormick, S.D., Shrimpton, J.M., and Zydlewski, J. 1996. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. *In* Global warming: implications for freshwater and marine fish. *Edited by* C.M. Wood and D.G. McDonald. Cambridge University Press, Cambridge. pp. 279–301.

McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **55**: 77–92.

Meeker, W.Q., and Escobar, L.A. 1998. Statistical methods for reliability data. John Wiley & Sons, New York.

Nettles, D.C., and Gloss, S.P. 1987. Migration of landlocked Atlantic salmon smolts and effectiveness of a fish bypass structure at a small-scale hydroelectric facility. N. Am. J. Fish. Manag. **7**: 562–568.

National Marine Fisheries Service (NMFS). 2000. Draft biological opinion: operation of the Federal Columbia River Power System including the Juvenile Fish Transportation Program and the Bureau of Reclamation's 31 projects, including the Entire Columbia Basin Project. National Marine Fisheries Service, Portland, Oreg.

Prentice, E.F., Flagg, T.A., and McCutcheon, S. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *In* Fish marking techniques. *Edited by* N.C. Parker, A.E. Giorgi, R.C. Heidinger, D.B. Jester, Jr., E.D. Prince, and G.A. Winans. American Fisheries Society, Bethesda, Md. pp. 317–322.

RMC Environmental Services. 1994. Movement and behavior of radio-tagged Atlantic salmon smolts at Wilder Hydroelectric Station, Spring, 1994. Report prepared for New England Power Company, Westborough, Mass.

SAS. 1999. SAS. SAS Institute Inc., Carey, N.C.

Shoenfeld, D. 1982. Partial residuals for the proportional hazards regression model. Biometrika, **69**: 239–241.

Skalski, J.R. 1998. Estimating season-wide survival rates of outmigrating salmon smolts in the Snake River, Washington. Can. J. Fish. Aquat. Sci. **55**: 761–769.

Skalski, J.R., Hoffmann, A., and Smith, S.G. 1993. Development of survival relationships using concomitant variables measured from individual smolt implanted with PIT-tags. U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg.

Skalski, J.R., Smith, S.G., Iwamoto, R.N., Williams, J.G., and Hoffmann, A. 1998. Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. Can. J. Fish. Aquat. Sci. **55**: 1484–1493.

Venditti, D.A., Rondorf, D.W., and Kraut, J.M. 2000. Migratory behavior and forebay delay of radio-tagged juvenile fall chinook salmon in a lower Snake River impoundment. N. Am. J. Fish. Manag. **20**: 41–52.

Whalen, K.G., Parrish, D.L., and McCormick, S.D. 1999. Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. Trans. Am. Fish. Soc. **128**: 289–301.

Wilson, J.W., Giorgi, A.E., and Stuehrenberg, L.C. 1991. A method for estimating spill effectiveness for passing juvenile salmon and its application at Lower Granite Dam on the Snake River. Can. J. Fish. Aquat. Sci. **48**: 1872–1876.

Zabel, R.W., and Anderson, J.J. 1997. A model of the travel time of migrating juvenile salmon, with an application to Snake River spring chinook salmon. N. Am. J. Fish. Manag. **17**: 93–100.

Zabel, R.W., Anderson, J.J., and Shaw, P.A. 1998. A multiple-reach model describing the migratory behavior of Snake River yearling chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **55**: 658–667.

Zydlewski, J., and McCormick, S.D. 1997*a*. The ontogeny of salinity tolerance in the American shad, *Alosa sapidissima*. Can. J. Fish. Aquat. Sci. **54**: 182–189.

Zydlewski, J., and McCormick, S.D. 1997*b*. The loss of hyperosmoregulatory ability in migrating juvenile American shad *Alosa sapidissima*. Can. J. Fish. Aquat. Sci. **54**: 2377–2387.

© 2003 NRC Canada

Mapping the abundance of riverine fish populations: integrating hierarchical Bayesian models with a geographic information system (GIS)

Robin J. Wyatt

Abstract: A hierarchical Bayesian model is described for mapping the abundance of fish throughout a watershed from single- and multiple-pass removal sampling. A geographic information system (GIS) was used to generate a raster-based model of the river network, which provided three benefits for estimating fish density. Firstly, the horizontal resolution of the raster (50 m) provided an approximation to the statistical sampling frame and allowed correction for the finite number of potential sampling sites in a reach. Secondly, the modelled river network generated explanatory variables for every site in the network, facilitating the mapping of predicted densities and providing the basis for stratified or regression estimators for reach-specific densities. Finally, the spatial autocorrelation of fish densities was modelled in terms of the distance along the river network. A similar Bayesian model was also developed for the wetted width of the river network, and this was combined with the density model to provide estimates of the total stock size. The model was implemented using Markov chain Monte Carlo simulation in the statistical package WinBUGS. Application of the hierarchical model is illustrated with electrofishing data for age-1+ sea trout (*Salmo trutta*) in a small tributary of the River Conwy, Wales.

Résumé : On trouvera ici un modèle hiérarchique bayésien qui sert à cartographier l'abondance des poissons dans un bassin versant à partir d'échantillonnages par retraits simples ou répétés. L'utilisation d'un système d'information géographique (GIS) permet de produire un modèle en trame du système hydrographique, qui présente trois avantages pour l'estimation de la densité des poissons. D'abord, la résolution horizontale de la trame (50 m) représente une approximation du plan statistique d'échantillonnage et permet de tenir compte du nombre fini de points potentiels d'échantillonnage dans une section. De plus, le modèle du réseau hydrographique génère des variables explicatives pour chaque point du réseau, ce qui facilite la cartographie des densités prédites et fournit une base pour les estimateurs stratifiés ou les estimateurs de régression des densités spécifiques aux sections. Enfin, l'autocorrélation spatiale des densités de poissons peut être modélisée en fonction de la distance le long du réseau hydrographique. Un modèle bayésien simple a aussi été mis au point pour estimer la largeur mouillée du réseau hydrographique; combiné au modèle de densité, il génère des estimations de la taille du stock total. Le modèle a été mis en opération en utilisant des simulations de Monte Carlo à l'aide de chaînes de Markov avec le logiciel statistique WinBUGS. Des données de pêche électrique de truites de mer (*Samo trutta*) de 1+ année d'un petit tributaire de la rivière Conwy, au Pays de Galles, servent à illustrer l'application du modèle hiérarchique.

[Traduit par la Rédaction]

Introduction

Geographic information systems (GIS) can greatly facilitate the design of spatial surveys and the analysis of spatial data (Burrough 2001). Their use in freshwater fisheries management is becoming more common, particularly in habitat classification and inventory studies and in describing the relationship between the distribution of fish and river habitat (Isaak and Hubert 1997; Kapetsky 2001).

Received 14 August 2002. Accepted 26 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 30 September 2003.
J17042

R.J. Wyatt. National Fisheries Technical Team, Environment Agency, Cambria House, 29 Newport Road, CF24 0TP, Cardiff, U.K. (e-mail: robin.wyatt@environment-agency.gov.uk).

Riverine fish populations are typically surveyed using two-stage sampling schemes in which a number of sites are first selected from the river reaches of interest and then the fish are sampled from each site. A GIS can be used to assist with the design of two-stage surveys and provide a rational basis for the selection of sites from a river network (Toepfer et al. 2000). However, in many situations, the fishery scientist will need to retrospectively analyse data that were collected for a possibly diverse set of objectives. The location and distribution of sampling sites may therefore be incompatible with the purpose for which they now need to be analysed, and sites may have been sampled using inconsistent methods. In this paper, the use of a GIS for the retrospective analysis of river fish population data is explored.

A GIS can be used to represent a river network in a range of formats, including polygons to represent areas of in-stream habitat features, a network of lines (vectors), or a network of pixels (raster). For mapping the longitudinal patterns of fish

 doi: 10.1139/F03-085 © 2003 NRC Canada

density within the river network, it is beneficial to model the river network from a grid of elevation data, called a digital elevation model (DEM). The DEM provides the basis for simple hydrologic modelling of a watershed (Hogg et al. 1993; Garbrecht and Martz 2000; Olivera et al. 2002) that for high-relief areas will generate a raster-based river network that traces the valley bottom. In low-relief areas, particularly with low vertical resolution DEMs, a vector river network may need to be "burned" into the DEM to provide a model of the river network that integrates the terrain data and the mapped course of the river (Saunders 2000).

The use of a raster-based model of the river network is fundamental to the statistical methods described in this paper and provides three major benefits for the estimation of fish density. Firstly, the horizontal resolution of the raster can be chosen so that the size of a single cell approximately corresponds to the length of a sampling site. The raster-based river network therefore provides an approximation to the statistical sampling frame of all possible sites from which the sample was drawn. This enables an estimate of population density for a reach to allow for both the actual number of sites sampled and the finite number of possible sites for which the estimate is required. Secondly, a river network modelled from a DEM offers the possibility for the automatic calculation of an almost limitless range of variables for every cell in the river network. This includes site-specific variables such as elevation and gradient, variables relating to the river path, such as stream order or distance to source, and variables relating to the drainage area upstream, such as land use or geology. Any relationships between these variables and the fish population density can be exploited to improve density estimates at sampled sites, unsampled sites, and the reach as a whole. Finally, the density of fish at a particular site is unlikely to be independent of the densities at adjacent sites because of fish movement and environmental factors not included in the model. The information from a GIS on the relative positions of sites within the river network can be utilised to model spatial autocorrelation, which will further improve the density estimates.

A spatial model can also be developed for the wetted width of the river network, which will allow for the finite size of river reaches, the relationship between width and GIS-generated covariates, and the autocorrelation of widths. This model can estimate the areas of habitat available and, by combining these with the density estimates, can provide estimates of the total population size.

A common method for estimating the population size of fish is the removal method in which fish are repeatedly removed from a closed population without replacement, using constant effort on each pass of a seine or electrofisher (Moran 1951; Zippin 1956; Carle and Strub 1978). The removal method is commonly used within the context of two-stage sampling schemes of river fish populations (Bohlin 1981; Hankin 1984). In these applications, estimation of the population size should take into account the between-site variation associated with the first stage of sampling and the within-site variation associated with the second stage of sampling. A common approach is to apply a removal estimator to the catch data from each site independently and then combine the site-specific estimates to give a population estimate for the entire reach. However, the application of a single hierarchical model to the combined catch data from all sites within the river reach will offer improved estimates for both the sampled sites and the reach as a whole and offer the added advantage of integrating data from both single- and multiple-pass sites (Wyatt 2002).

Hierarchical models can be implemented using either frequentist or Bayesian inference. The Bayesian approach (O'Hagan 1994; Gelman et al. 1995; Carlin and Louis 2000) has the advantage that prior information for model parameters can be integrated with sample data and that direct probabilistic statements can be made about the population size, conditional on the particular data set (Barnett 1999). However, Bayesian analysis can present computational difficulties and requires the use of computer-intensive techniques such as sampling-importance resampling methods (SIR; Rubin 1988; Smith and Gelfand 1992), or Markov chain Monte Carlo methods (MCMC; Gilks et al. 1996; Brooks 1998). Until recently, the need for such techniques presented an obstacle to the routine use of Bayesian methods in the analysis of fish population data. However, general-purpose statistical packages that implement MCMC routines are now becoming widely available.

The objective of this study was to combine four powerful approaches towards the estimation and mapping of riverine fish abundance: GIS-based river modelling, hierarchical modelling of catches from the removal method, Bayesian inference, and the use of MCMC software. The starting point was a hierarchical Bayesian model similar to that of Wyatt (2002), which can be implemented without a GIS (model I). The model was then refined by incorporating a GIS-derived sampling frame (model II), GIS-derived explanatory variables for density (model III), and spatial autocorrelation in density (model IV). The relationship between capture probability and site characteristics was also explored (model V). Finally, a similar approach was used to model the width of the river, and the width model was then combined with the density model to derive estimates of the population size (model VI).

Methods

Specification of basic fish density model (model I)

The fish population survey consists of sampling M sites, and at the ith site ($i = 1, 2, \ldots, M$), K_i passes are undertaken ($K_i \geq 1$), and for each species and age class, a catch c_{ij} is obtained on the jth pass ($j = 1, \ldots, K_i$). The number of fish captured on the jth pass (c_{ij}) will follow a binomial distribution

$$(1) \qquad c_{ij} \sim \text{Binomial}(n_{ij}, p_i)$$

where n_{ij} is the number of fish present prior to the jth pass, and p_i is the capture probability for all individuals on each pass. The number of fish remaining after the jth pass is then

$$(2) \qquad n_{i,j+1} = n_{ij} - c_{ij}$$

These two equations describe the binomial model for the within-site variation in catches on which simple removal estimators are based (Moran 1951; Zippin 1956; Carle and Strub 1978). To develop a hierarchical model for the data obtained from removal sampling, it is necessary to construct a model for the between-site variation in the capture probability and population density.

© 2003 NRC Canada

The between-site variation in the logistic transformation of the capture probability was assumed to follow a normal distribution, with unknown mean (μ_p) and variance (σ_p^2)

$$\text{(3)} \quad \text{logit}(p_i) \sim \text{Normal}(\mu_p, \sigma_p^2)$$

The between-site variation in the log population density was also assumed to follow a normal distribution, with unknown mean (μ_d) and variance (σ_d^2)

$$\text{(4)} \quad \log(d_i) \sim \text{Normal}(\mu_d, \sigma_d^2)$$

The population size at a site before the first pass is given by

$$\text{(5)} \quad n_{i1} \sim \text{Poisson}(d_i w_i l_i)$$

where w_i and l_i are the width and length of the sampling site, respectively.

Estimates of the population size within a river reach can be based on the estimate of the parameter μ_d. For example, if the mean width of the river network is $\overline{w}$, a naive estimate of the population size (n_r) of the rth reach ($r = 1,2,\ldots,G$) of length l_r within the target area could be given by

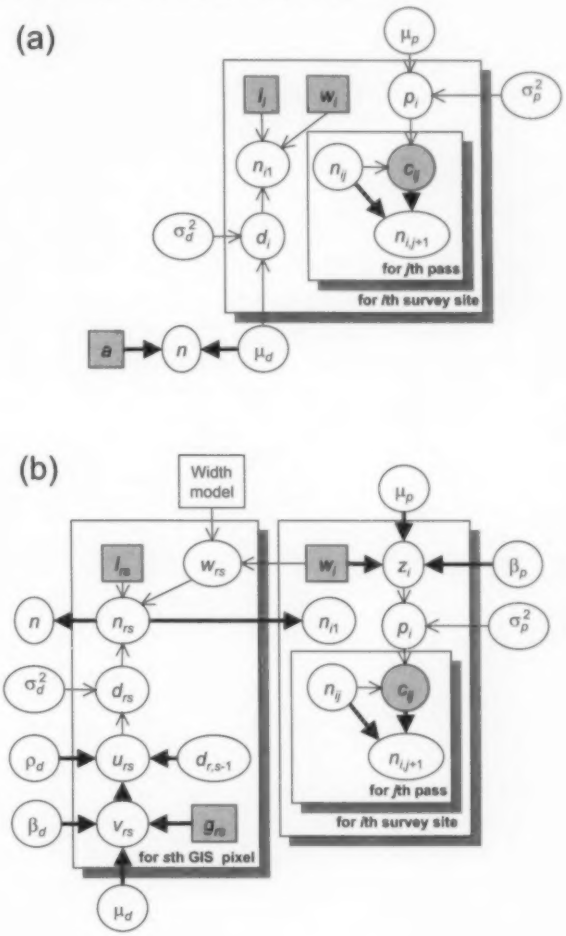
$$\text{(6)} \quad n_r = l_r \mu_d \overline{w}$$

and the population size for the target area is given by

$$\text{(7)} \quad n = \sum_{r=1}^{G} n_r$$

This model can be illustrated by a directed acyclic graph (DAG; Fig. 1*a*) in which the nodes denote model components and the arrows denote the stochastic (thin arrows) and deterministic (thick arrows) dependencies between them. Observed nodes are shaded, unobserved nodes are unshaded, and explanatory variables, such as the total target area (a) of the reach, are shown as squares. Model components that are repeated over different sites (i) and passes (j) are enclosed within the rectangular plates. This model is similar to the hierarchical model of Wyatt (2002) but with a normal distribution for $\log(d_i)$ replacing a gamma distribution for d_i and a normal distribution for $\text{logit}(p_i)$ replacing a beta distribution for p_i. This model does not require a GIS.

Fig. 1. Graphical representation of two hierarchical models for removal data: (*a*) model I, simple model for random variation in density (d_i) and capture probability (p_i); and (*b*) model VI, geographic information system (GIS) based model including the influence of gradient (g_{rs}) and autocorrelation (ρ_d) on density and the influence of width (w_i) on capture probability.



Derivation of river network

Derivation of the river network was undertaken using ArcView GIS 3.1, ArcView Spatial Analyst 1.1, and the Hydrologic Modelling Extension 1.1 (ESRI, Redlands, Calif.). All calculations were performed using the built-in functionality of the software and did not require the development of specialised computer code. The starting point for the modelling was a DEM for the watershed of interest, with a 50-m horizontal resolution and 3-m vertical resolution. Areas of internal drainage ("sinks") were identified and filled. The flow direction and slope at each 50-m cell were calculated from the elevation data, and the catchment area upstream of each cell (flow accumulation) was then calculated from the flow direction. The river network was modelled by defining it as cells that had a flow accumulation greater than some threshold value, which was chosen to give close visual agreement with the mapped 1 : 50 000 scale river network. In large watersheds with diverse geology, the watershed was subdivided into homogenous areas, and different flow accumulation thresholds were set for each. Reaches within the derived river network were assigned a unique stream link number (r), and the stream order (o) was calculated for each reach. The flow accumulation, slope, stream link, flow direction, and stream order for each cell were exported from ArcView for further manipulation. Each cell within a reach was assigned a site index s ($s = 1,2,\ldots,H_r$) according to the flow accumulation (i.e., lowest flow accumulation had index 1), and the combination of the stream link number (r) and the site index (s) therefore provided a unique identifier for each cell. The flow direction was used to assign lengths (l_{rs}) to each cell: 50 m for cells flowing horizontally or vertically and 71 m for cells flowing diagonally.

Sampling frame (model II)

In model I, the uncertainty associated with the estimated population size of a reach (n_r) was obtained directly from

© 2003 NRC Canada

the uncertainty associated with μ_d and did not allow for the potential number of sampling sites. In model II, the river was regarded as having been divided into a finite number of sites from which the sample was drawn (Bohlin 1981; Hankin 1984). At one extreme, all potential sites within a reach may have been sampled, and the only source of uncertainty would be binomial sampling error associated with the second stage of sampling. At the other extreme, the uncertainty associated with predicting the population size of a single unsampled site should include not only the uncertainty associated with the underlying mean (μ_d), but also the between-site variance of densities about the mean (σ_d^2). An estimate based on μ_d alone (model I) will therefore overestimate the uncertainty in the first scenario but underestimate it in the second.

With a GIS, the population size at all sites (sampled and unsampled) within the target area could be considered, and eq. 4 was replaced by

$$\log(d_{rs}) \sim \text{Normal}(\mu_d, \sigma_d^2) \quad (8)$$

The width of each unsampled site was assumed to be equal to the mean width of the sampled sites:

$$w_{rs} = \overline{w} \quad (9)$$

The population size in a GIS cell was therefore given by

$$n_{rs} \sim \text{Poisson}(d_{rs} w_{rs} l_{rs}) \quad (10)$$

The population size for a reach was obtained by replacing eq. 6 with

$$n_r = \sum_{s=1}^{H_r} n_{rs} \quad (11)$$

Relationship between density and map-based variables (model III)

If a relationship exists between fish density and map-based variables available from a GIS, then this can be exploited to improve the density estimates through stratification or the use of regression estimators. A regression estimator was used by replacing eq. 8 with

$$\log(d_{rs}) \sim \text{Normal}(v_{rs}, \sigma_d^2) \quad (12)$$

where v_{rs} is some function of any combination of map-based variables available from a GIS for every site within the river network. To illustrate the method, a linear function of site gradient (g_{rs}) was used:

$$v_{rs} = \mu_d + \beta_d g_{rs} \quad (13)$$

Spatial autocorrelation in density (model IV)

Model III made the assumption that the densities of fish in each cell (d_{rs}) were independent of each other (eq. 12). However, the use of a GIS allows the modelling of spatial autocorrelation because the indexing of reaches and sites within reaches provides information of the spatial relationships of cells within the river network. An autoregressive model with lag 1 (AR1) was assumed, providing a simple model in which distance between sites was not defined in terms of linear distance, but in terms of the distance along the river network. At the first site ($s = 1$) in a first-order stream ($o = 1$), no dependence with an upstream site can be defined. However, at all other sites, the log density ($\log(d_{rs})$) was assumed to be correlated (ρ_d^2) with the log density upstream ($\log(d_{r,s-1})$), which at a confluence ($s = 1$, $o > 1$) was defined as the average of the log densities at the sites immediately upstream. Equation 12 was replaced by

$$\log(d_{rs}) \sim \begin{cases} \text{Normal}(v_{rs}, \sigma_d^2), s = 1, o = 1 \\ \text{Normal}(u_{rs}, \phi_d^2), \text{otherwise} \end{cases} \quad (14)$$

where the expected log density (u_{rs}) at a site is a weighted average of the log density predicted by the gradient (v_{rs}) and the log density at the site immediately upstream ($\log(d_{r,s-1})$):

$$u_{rs} = (1 - \rho_d) v_{rs} + \rho_d \log(d_{r,s-1}) \quad (15)$$

and ϕ_d^2 is the variance about this expected value:

$$\phi_d^2 = \sigma_d^2 (1 - \rho_d^2). \quad (16)$$

Thus for a ρ_d close to one, the expected value at a site will be similar to the upstream density, and the variance (ϕ_d^2) around the expected value will be small. Conversely, for a ρ_d close to zero, the expected value at a site will be close to that predicted by the gradient (v_{rs}), and the variance around the expected value will be close to σ_d^2.

Relationship between capture probability and map- or field-based variables (model V)

The capture probability of the removal process may also be influenced by site-specific variables. However, unlike density, explanatory variables for capture probability are only required for the sampled sites and may therefore be obtained from field-based measurements or a GIS. Equation 3 was replaced by

$$\text{logit}(p_i) \sim \text{Normal}(z_i, \sigma_p^2) \quad (17)$$

where z_i is some function of any GIS-derived or field-based variables measurable at the sampling sites. To illustrate the method, a linear function of wetted width (w_i) was used:

$$z_i = \mu_p + \beta_p w_i \quad (18)$$

Addition of width model (model VI)

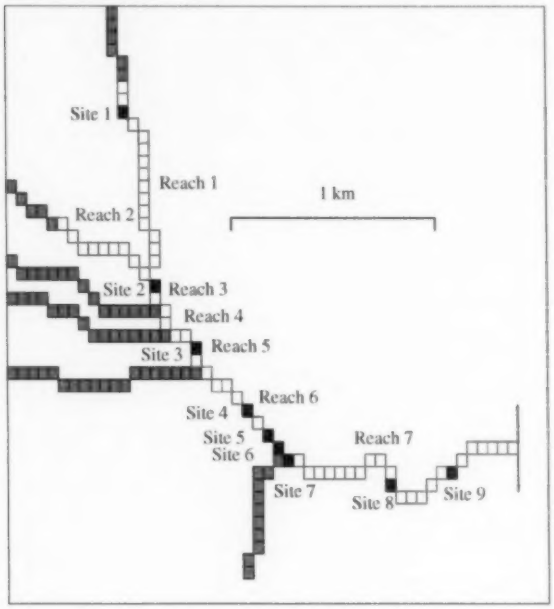
Spatial variation in width had not been addressed in models I to V, and although it will not influence the estimation and mapping of density, it may strongly influence the estimation of population size. The information provided by a GIS on the number of cells within a reach, environmental variables for each cell, and the spatial relationship between cells can be utilised to develop a model for river width and therefore wetted area. The model for width followed the approach used for fish density; it differed primarily in that the width at a sampled site was assumed to be known, and therefore the model was not hierarchical. Equation 9 was replaced by the following model:

$$\log(w_{rs}) \sim \begin{cases} \text{Normal}(y_{rs}, \sigma_w^2), s = 1, o = 1 \\ \text{Normal}(x_{rs}, \phi_w^2), \text{otherwise} \end{cases} \quad (19)$$

where y_{rs} is the log width predicted from the flow accumulation (f_{rs}):

© 2003 NRC Canada

Fig. 2. Raster-based model of the Nant-y-Goron. Direction of flow is from top left to bottom right. Sites sampled by electrofishing are shown in black, and sites inaccessible to migratory fish are shown in grey.



$$y_{rs} = \mu_w + \beta_w \log(f_{rs}) \quad (20)$$

x_{rs} is the expected log width at a site, given the upstream log width ($\log(w_{r,s-1})$) and autocorrelation (ρ_w^2):

$$x_{rs} = (1 - \rho_w) y_{rs} + \rho_w \log(w_{r,s-1}) \quad (21)$$

and ϕ_w^2 is the variance about this expected value:

$$\phi_w^2 = \sigma_w^2 (1 - \rho_w^2) \quad (22)$$

The upstream log width ($\log(w_{r,s-1})$) at a confluence ($s = 1$, $o > 1$) was defined as the square root of the sum of the squared log widths at the sites immediately upstream. The total wetted area of a reach is given by

$$a_r = \sum_{s=1}^{H_r} l_{rs} w_{rs} \quad (23)$$

and the wetted area of the target area is given by

$$a = \sum_{r=1}^{G} a_r \quad (24)$$

A DAG for model VI (Fig. 1*b*) helps to illustrate the structure of the model in relation to the simpler model I (Fig. 1*a*). The DAG for model VI comprises two sets of plates: the right-hand plates enclose the M sampling sites and the K_i passes undertaken within them, and the left-hand plate encloses the H_r sites (GIS pixels) within each of the G reaches. The total population size (n) can therefore be estimated by summing the population estimates (n_{rs}) over the finite number of sites in each reach. The density at every site (d_{rs}) is related to the gradient of the site (g_{rs}) by an additional parameter (β_d). Similarly, the capture probability at the sampled sites is related to the width of the sampled site (w_i) by an additional parameter (β_p). Finally, the density of fish at each site (d_{rs}) is related to the density at the site immediately upstream ($d_{r,s-1}$) by the level of autocorrelation (ρ_d).

Table 1. Catch data for age-1+ sea trout (*Salmo trutta*) from nine sites on the Nant-y-Goron, Wales.

		Catches			
Site (i)	Width (w_i; m)	c_{i1}	c_{i2}	c_{i3}	c_{i4}
1	2.10	14	7	—	—
2	3.38	5	4	1	—
3	2.73	17	5	1	—
4	3.12	14	4	0	—
5	4.58	22	5	0	—
6	2.28	11	2	0	—
7	5.12	17	11	2	—
8	3.35	6	1	0	0
9	2.98	3	0	0	—

Application

The approach is illustrated with data from an electrofishing survey of age-1+ sea trout (*Salmo trutta*), upstream of a smolt-trapping site on the Nant-y-Goron, a small tributary of the River Conwy, Wales. The GIS-derived river network for the Conwy was defined at cells with a flow accumulation greater than 60. The target area of interest comprised 3.8 km of stream accessible to adult sea trout, with an average wetted width of 3.3 m (Fig. 2). Nine 50-m sites were selected at random, and removal sampling was undertaken at each site, with between two and four passes (Table 1).

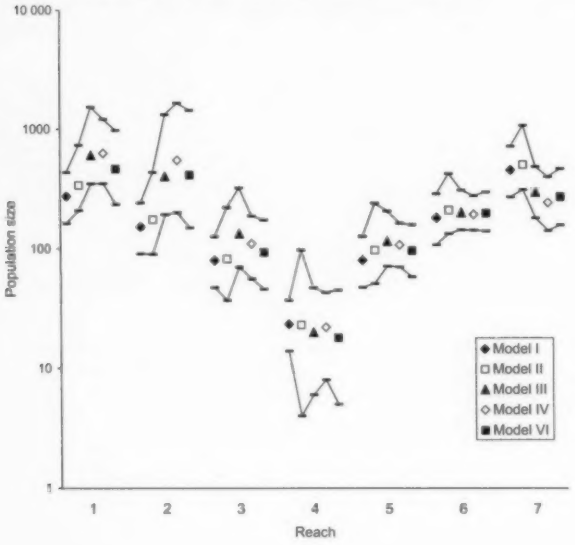
Minimally informative normal priors (Normal($0, 1 \times 10^6$)) were chosen for many of the model parameters (μ_d, μ_p, μ_w, β_d, β_p), whereas the parameter describing the relationship between width and flow (β_w) was constrained to be positive (Uniform(0, 10)). Minimally informative priors (Gamma(0.001, 0.001) were chosen for the inverse of the variances (σ_d^2,σ_p^2,σ_w^2), and uniform priors (Uniform(-1, 1)) were chosen for autocorrelation parameters (ρ_d, ρ_w).

Models I to VI were implemented using WinBUGS 1.4 (Gilks et al. 1994; Spiegelhalter et al. 2003); the WinBUGS code is available from the author upon request. Convergence was monitored with the Gelman and Rubin (1992) convergence statistic, as modified by Brooks and Gelman (1998). Two Markov chains were used, and after a burn-in period of 4000 iterations, inference was based on the two chains each of length 50 000. Posterior distributions for model I were also checked by comparison with the approximate analytical solution of Wyatt (2002).

A number of checks on the fit of the model can be undertaken within WinBUGS. An important criterion for the current application is the ability of the model to predict densities at unsampled sites, and this was investigated by cross-validation. The model was recalibrated nine times with the catch data from each of the nine sampled sites removed from the analysis in turn. For each site, the density predicted from the remaining

© 2003 NRC Canada

Fig. 3. Population estimates (n_r) for the seven reaches of the Nant-y-Goron from five models (I, II, III, IV, and VI). Horizontal lines indicate 95% posterior probability intervals.



eight sites could then be compared with the density estimated from the full data set.

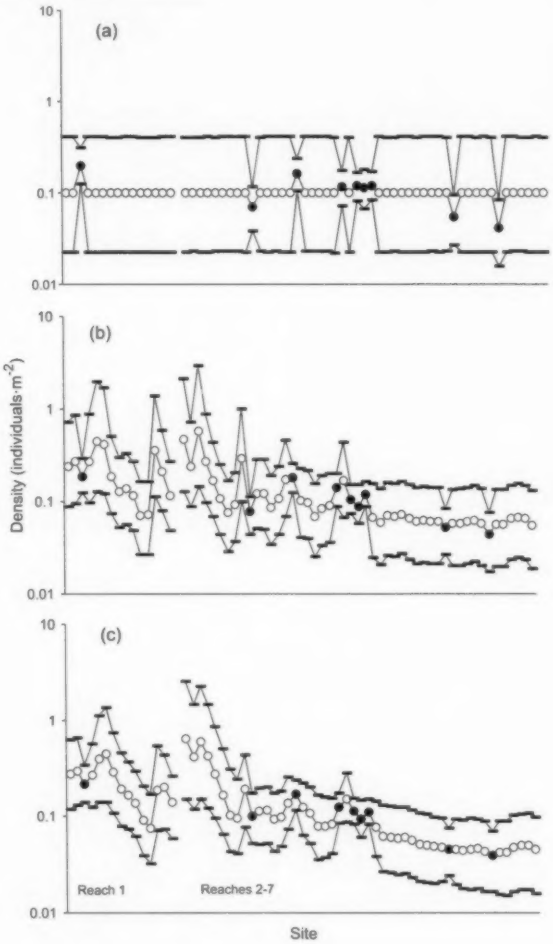
Results

The population estimates from model I for the seven reaches of the Nant-y-Goron primarily reflected the different lengths of the reaches (Fig. 3). With model II, estimates of the population density were available at all sites within the target area (Fig. 4*a*), and at these unsampled sites, the estimated densities (d_{rs}) corresponded to the underlying mean density (μ_d). Assessment of the population size by summing over the finite number of potential sampling sites in each reach gave a slight increase in the population estimate (Fig. 3), and the uncertainty increased, particularly in the shorter reaches (e.g., reaches 3 to 5). There was a significant positive relationship between density and the GIS-derived gradient of the site (model III; Table 2). Density estimates at unsampled sites therefore increased in the high-gradient upper sites and decreased in the low-gradient lower sites, and the variance of the model III estimates decreased (Fig. 4*b*). These changes were also reflected in the estimates of population size for the seven reaches (Fig. 3). Having allowed for the influence of gradient, there was evidence for additional positive autocorrelation in density (model IV; Table 2). Inclusion of autocorrelation in model IV resulted in a smoothed pattern of interpolated densities (Fig. 4*c*) and a generally lower uncertainty in the site-specific density estimates (Fig. 4*c*) and the reach-specific population estimates (Fig. 3).

On the Nant-y-Goron, there was no discernible relationship between capture probability and the wetted width (model V; Table 2), and so site width was not included in the capture-probability component of subsequent models.

The cross-validation showed that the predicted densities from model IV for each site were in reasonable agreement

Fig. 4. Density estimates (d_{rs}) from models II, III, and IV for the Nant-y-Goron. Open circles denote unsampled sites; solid circles denote sampled sites. Horizontal lines indicate 95% posterior probability intervals.



with the estimated densities (Fig. 5) and occurred within a range of between 0.05 and 0.2·m^{-2}. The largest discrepancy between estimated and predicted densities occurred at site 2, at which the predicted density was nearly twice that estimated from the full data set. The widths of the 95% probability intervals were considerably greater for the predictions than for the estimates for most sites. The exception was site 6 for which the interval for the prediction was only slightly greater than that for the estimate because of the proximity to sites 5 and 7 and the presence of a positive autocorrelation.

Once the model had been validated, the density estimates at all sites (Fig. 4*c*) could be used as the basis for mapping estimated density (Fig. 6*a*) and mapping the uncertainty associated with density estimation (Fig. 6*b*). The model also provided estimates of the population size (n_{i1}) and the capture probability (p_i) at the sampled sites (Table 3).

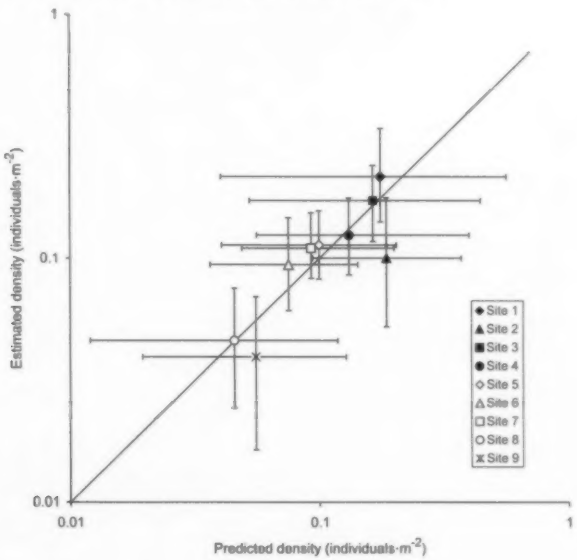
To improve the estimates of the total population size within a reach, the density model was combined with a width

© 2003 NRC Canada

Table 2. Summary of the posterior probability distributions for the parameters of the density models.

Parameter	Percentile	Models I and II	Model III	Models IV and VI	Model V
Density					
Mean (μ_d)	2.5	−2.821	−2.556	−2.840	−2.770
	50.0	−2.304	−2.214	−2.300	−2.266
	97.5	−1.844	−1.923	−2.024	−2.016
Variance (σ_d^2)	2.5	0.0739	0.0020	0.0013	0.0010
	50.0	0.3369	0.0898	0.0527	0.0343
	97.5	1.4524	0.6398	0.5482	0.4193
Gradient parameter (β_d)	2.5	—	0.06544	0.08751	0.1039
	50.0	—	0.1864	0.2376	0.2390
	97.5	—	0.3387	0.4020	0.3893
Autocorrelation (ρ_d)	2.5	—	—	−0.0638	0.01252
	50.0	—	—	0.5235	0.5481
	97.5	—	—	0.8913	0.9058
Capture probability					
Mean (μ_p)	2.5	0.238	0.2705	0.1386	−0.07112
	50.0	0.7438	0.7393	0.730	0.7168
	97.5	1.205	1.204	1.230	1.312
Variance (σ_p^2)	2.5	0.0008	0.0008	0.0009	0.0010
	50.0	0.0310	0.0327	0.0486	0.1236
	97.5	1.0120	0.9017	1.7042	3.1368
Width parameter (β_p)	2.5	—	—	—	−0.6362
	50.0	—	—	—	−0.0365
	97.5	—	—	—	0.6378

Fig. 5. Density estimates at sampled sites (d_i) and densities predicted by cross-validation of model IV. Horizontal and vertical bars indicate 95% posterior probability intervals.



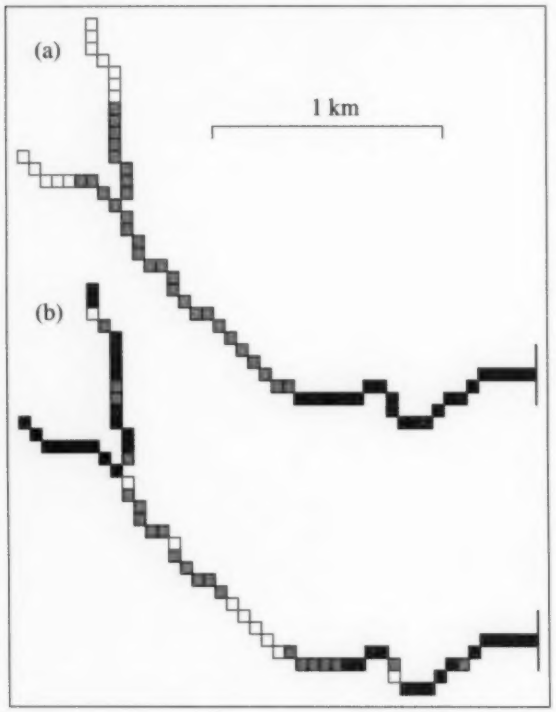
model (model VI). There was a 95% probability that the flow parameter (β_w) was between 0.03 and 0.69 (Table 4), and so widths increased approximately in proportion to the square-root ($\beta_w = 0.5$) of the upstream catchment area. The width model also provided evidence for negative autocorrelation (Table 4) because of the large differences between the widths of adjacent sites (e.g., sites 5, 6, and 7; Table 1). This probably reflects the riffle–pool sequence in the Nant-y-Goron. The combination of the width model and the density model (model VI) resulted in a decline in the population estimates in the narrower upper reaches and a corresponding increase in population estimates in the wider, lower reaches (Fig. 3). There was a 95% probability that the total population (n) of age-1+ trout in the Nant-y-Goron was between 1057 and 3162, and as would be expected, this estimate was correlated with the estimate of the total wetted area (a) (Fig. 7).

Discussion

A GIS provides an invaluable tool for modelling the spatial patterns of riverine fish populations. In particular, a GIS can economically provide data on the characteristics of every potential sampling site in the river network, exemplified on the Nant-y-Goron by gradient and drainage area. Relationships between these GIS-derived variables and fish density can then be used to predict the densities at unsampled sites and thus map the spatial patterns in density throughout the river network. Furthermore, knowledge of the GIS-derived variables for every site in the river network facilitates the use of stratification, or regression estimators, to improve the estimation of the total population size within a river reach. For these applications, it is necessary to have

© 2003 NRC Canada

Fig. 6. Map of (*a*) age-1+ trout (*Salmo trutta*) density estimates (d_{rs}) and (*b*) prediction errors from model IV for the Nant-y-Goron. Density in (*a*) is classified as low (d_{rs} < 0.07 individuals (ind.)·m^{-2}, solid squares), moderate (0.07 ind.·m^{-2} < d_{rs} < 0.21 ind.·m^{-2}, shaded squares), and high (d_{rs} > 0.21 ind.·m^{-2}, open squares). Precision in (*b*) is classified in terms of the standard error of the log density (SE) as low (SE > 0.4, solid squares), moderate (0.3 < SE < 0.4, shaded squares), and high (SE < 0.3, open squares).



data on the explanatory variables at both the sampled and unsampled sites in the river network; something that a GIS can provide but field surveys of river habitat may not.

The interpolation or smoothing of spatial fishery data is commonly achieved using geostatistical techniques such as kriging (Rivoirard et al. 2000), in which the spatial correlation between pairs of points is related to the distance between them by a variogram. In this study, the use of a GIS to represent the river network as a chain on 50-m cells allowed the use of a much simpler spatial correlation structure (AR1). However, the approach used here has a number of advantages in the context of small-scale surveys of river networks. Firstly, the distance between sampling sites is not measured in terms of linear distance, but in terms of the distance along the river network. This is appropriate in situations in which sites that are geographically close to each other would not necessarily be expected to show spatial correlation, as for example, when they are in neighbouring watersheds. Secondly, the covariance structure (variogram) in kriging is assumed to be exactly known and therefore requires a large sample size. The prediction of density in this study uses Bayesian inference to fully integrate the high estimation error for the spatial variance and autocorrelation, associated with the very small sample size (Le and Zidek 1992; Handcock and Stein 1993). Finally, the approach described here involves a nonnormal hierarchical model and so in this respect resembles a model-based approach to geostatistics (Diggle and Tawn 1998).

The use of a GIS to correct for the finite number of potential sampling sites will only make a substantial difference to the estimated precision in intensive stream surveys in which the proportion of the stream surveyed is high or population estimates for small subreaches are required. On the Nant-y-Goron, a relatively high number of sites were sampled rela-

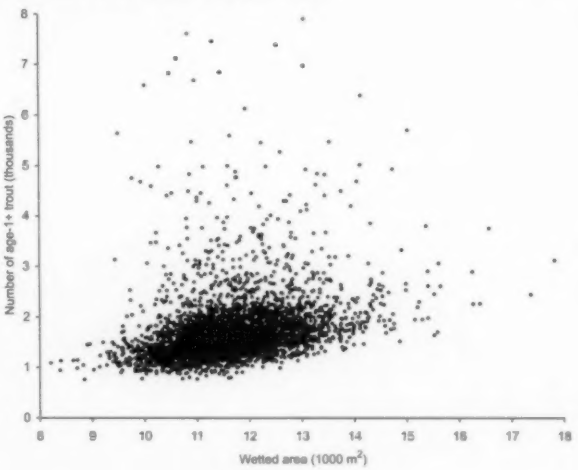
Table 3. Percentiles of the posterior probability distributions for the site-specific population size (n_i) and capture probability (p_i) using model IV.

	n_i			p_i		
Site (*i*)	2.5%	50.0%	97.5%	2.5%	50.0%	97.5%
1	21	24	33	0.412	0.660	0.774
2	10	11	25	0.187	0.643	0.758
3	23	24	27	0.539	0.681	0.803
4	18	19	21	0.549	0.689	0.835
5	27	28	30	0.587	0.705	0.856
6	13	13	15	0.557	0.694	0.864
7	30	31	36	0.473	0.651	0.753
8	7	7	8	0.505	0.685	0.856
9	3	3	6	0.370	0.674	0.848

Table 4. Summary of the posterior probability distributions for the parameters of the width model.

	Percentile		
Parameter	2.5	50.0	97.5
Mean (μ_w)	0.8801	1.078	1.250
Variance (σ_w^2)	0.0231	0.0613	0.2663
Flow parameter (β_w)	0.03435	0.2856	0.6864
Autocorrelation (ρ_w)	–0.9195	–0.5408	0.1927

Fig. 7. Sample of 4000 numbers from the joint posterior distribution for the population (*n*) of age-1+ trout (*Salmo trutta*) and the wetted area of the Nant-y-Goron.



© 2003 NRC Canada

tive to the finite number of potential sampling sites, and population estimates were reported separately for short reaches within the target area. In this example, the finite population correction was therefore considered worthwhile, but for surveys that operate on a more extensive spatial scale, this correction may make little difference.

The application of a hierarchical model to the combined catch data from all sites provides a natural way to analyse data from a two-stage sampling scheme compared with the repeated application of a removal estimator to the data from individual sites (Wyatt 2002). For example, a hierarchical model provides a means of integrating sites for which the catch data provide little information on the site-specific population size, such as sites at which few fish were captured or a low number of passes were undertaken. The use of a hierarchical model therefore enables the estimation and mapping of fish abundance across a wide spatial scale from surveys comprising a mixture of multiple-pass and lower-cost single-pass removal sampling. The site-specific population estimates will also be improved and will take into account autocorrelation and explanatory environmental variables.

A Bayesian approach to data analysis offers two potential benefits for the mapping of riverine fish abundance. Firstly, Bayesian inference provides a probability distribution for all model parameters and predictions, conditional on the particular data set observed, and so provides a basis for formal decision-making in fisheries management (Punt and Hilborn 1997; McAllister and Kirkwood 1998). Secondly, Bayesian inference has the ability to combine prior information for model parameters with sample data. In the model for the Nant-y-Goron, the prior distributions for most parameters were chosen to be minimally informative, and yet the number of sampling sites was too small to provide precise estimates of some of the model parameters. For certain key parameters specific to the Nant-y-Goron, such as the underlying population density (μ_d) in the year of survey, it would have been inappropriate to use prior information from other surveys. However, for other parameters, such as those describing the relationship between population density and site gradient (β_d) or the degree of autocorrelation between adjacent sites (ρ_d), it may have been acceptable to use prior information obtained from other more extensive surveys of similar river types (Punt and Hilborn 1997). The only use of an informative prior was in the width model in which the relationship between wetted width and flow accumulation (β_w) is known to be positive, even if this underlying relationship is not observable with few observations over a short length of stream.

The use of a statistical package such as BUGS enables fishery scientists to concentrate on the development of realistic Bayesian models, without the need for programming computer-intensive routines such as MCMC (Meyer and Millar 1999; Millar and Meyer 2000). It would therefore be relatively straightforward to refine the model to include a greater degree of realism where the data permit. For example, if a larger number of sites are selected at the first stage of sampling, more realistic models relating fish density or capture probability to environmental variables could be developed. Similarly, if a larger number of passes are undertaken at the second stage of sampling, it would be possible to modify the BUGS code to allow for different capture probabilities between individual fish or changing capture probabilities between successive passes. The model presented here was developed for an intensive survey of a small stream in which considerations such as finite population correction may be important for the estimation of the total population size within a reach. There is no statistical reason why the model could not be applied to a larger spatial scale, although the volumes of data obtained from the pixelation of the river network may become excessive, particularly given the use of computer-intensive MCMC methods. However, the power and flexibility of a GIS combined with a Bayesian modelling language will facilitate the development of statistical models tailored to the available data, spatial scale, and survey objectives.

Acknowledgments

This work was encouraged and reviewed by Mike Nicholson, who tragically died before its publication. He will be greatly missed in the world of fisheries statistics. Funding for this work was provided by the Environment Agency Research and Development Programme. Elevation data and river network maps were obtained from the Ordnance Survey with the permission of the Controller of Her Majesty's Stationery Office (© Crown Copyright, Licence No. GD 03177G). The electrofishing data for the Nant-y-Goron were provided by Ian Davidson. The improvements suggested by the anonymous referees are gratefully acknowledged. The views expressed by the author are not necessarily those of the Environment Agency.

References

Barnett, V. 1999. Comparative statistical inference. 3rd ed. John Wiley & Sons Ltd., Chichester, U.K.

Bohlin, T. 1981. Methods of estimating total stock, smolt output and survival of salmonids using electrofishing. Rep. Inst. Freshw. Res. Drottningholm, **59**: 5–14.

Brooks, S.P. 1998. Markov chain Monte Carlo method and its application. Statistician, **47**: 69–100.

Brooks S.P., and Gelman, A. 1998. Alternative methods for monitoring convergence of iterative simulations. J. Comput. Graph. Statist. **7**: 434–455.

Burrough, P.A. 2001. GIS and geostatistics: essential partners for spatial analysis. Environ. Ecol. Stat. **8**: 361–377.

Carle, F.L., and Strub, M.R. 1978. A new method for estimating population size from removal data. Biometrics, **34**: 621–630.

Carlin, B., and Louis, T. 2000. Bayes and Empirical Bayes methods for data analysis. 2nd ed. Chapman and Hall, London.

Diggle, P.J., and Tawn, J.A. 1998. Model-based geostatistics. Appl. Stat. **47**: 299–350.

Garbrecht, J., and Martz, L.W. 2000. Digital Elevation Model issues in water resource modelling. *In* Hydrologic and hydraulic modelling support with Geographic Information Systems. *Edited by* David Maidment and Jean Djokic. ESRI Press, Redlands, Calif.

Gelman, A., and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences (with discussion). Stat. Sci. **7**: 457–511.

Gelman, A., Carlin, J., Stern, H., and Rubin, D. 1995. Bayesian data analysis. Chapman and Hall, London.

Gilks, W.R., Thomas, A., and Spiegelhalter, D.J. 1994. A language and program for complex Bayesian modelling. Statistician, **43**: 169–178.

© 2003 NRC Canada

Gilks, W.R., Richardson, S., and Spiegelhalter, D.J. (*Editors*). 1996. Markov Chain Monte Carlo in practice. Chapman and Hall, London.

Handcock, M.S., and Stein, M.L. 1993. A Bayesian analysis of kriging. Technometrics, **35**: 403–410.

Hankin, D.G. 1984. Multistage sampling designs in fisheries research: application in small streams. Can. J. Fish. Aquat. Sci. **41**: 1575–1591.

Hogg, J., McCormack, J.E., Roberts, S.A., Gahegan, M.N., and Hoyle, B.S. 1993. Automated derivation of stream-channel networks and selected catchment characteristics from digital elevation models. *In* Geographical information handling — research and applications. *Edited by* Paul M. Mather. John Wiley & Sons Ltd., New York.

Isaak, D.J., and Hubert, W.A. 1997. Integrating new technologies into fisheries science: the application of geographic information systems. Fisheries, **22**: 6–10.

Kapetsky, J.M. 2001. Recent applications of GIS in inland fisheries. *In* Proceedings of the First International Symposium on GIS in Fishery Science. *Edited by* Tom Nishida, Chuck E. Hollingworth, and Patricia J. Kailola. Fishery/Aquatic GIS Research Group, Kawagoe-City, Japan.

Le, N.D., and Zidek, J.V. 1992. Interpolation with uncertain spatial covariances: a Bayesian alternative to kriging. J. Multivariate Anal. **43**: 351–374.

McAllister, M.K., and Kirkwood, G.P. 1998. Bayesian stock assessment: a review and example application using the logistic model. ICES J. Mar. Sci. **55**: 1031–1060.

Meyer, R., and Millar, R. 1999. BUGS in Bayesian stock assessment. Can. J. Fish. Aquat. Sci. **56**: 1078–1086.

Millar, R.B., and Meyer, R. 2000. Bayesian state–space modeling of age-structured data: fitting a model is just the beginning. Can. J. Fish. Aquat. Sci. **57**: 43–50.

Moran, P.A.P. 1951. A mathematical theory of animal trapping. Biometrika, **38**: 307–311.

O'Hagan, A. 1994. Kendall's advanced theory of statistics. Vol. 2b. Bayesian inference. Edward Arnold Publishers Ltd., London.

Olivera, F., Furnans, J., Maidment, D., Djokic, D., and Ye, Z. 2002. Drainage systems. *In* Arc Hydro: GIS for water resources. *Edited by* David Maidment. ESRI Press, Redlands, Calif.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**: 35–63.

Rivoirard, J., Simmonds, J., Foote, K.G., Fernandes, P., and Bez, N. 2000. Geostatistics for estimating fish abundance. Blackwell Science Ltd., Oxford.

Rubin, D.B. 1988. Using the SIR algorithm to simulate posterior distributions. *In* Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1–5, 1987. *Edited by* J.M. Bernardo, M.N. Degroot, D.V. Lindley, and A.M. Smith. Clarendon Press, Oxford. pp. 385–402.

Saunders, W. 2000. Preparation of DEMs for use in environmental modelling analysis. *In* Hydrologic and hydraulic modelling support with Geographic Information Systems. *Edited by* David Maidment and Jean Djokic. ESRI Press, Redlands, Calif.

Smith, A.F.M., and Gelfand, A.E. 1992. Bayesian statistics without tears: a sampling–resampling perspective. Am. Stat. **46**: 84–88.

Spiegelhalter, D., Thomas, A., Best, N., and Lunn, D. 2003. WinBUGS user manual. Ver. 1.4. Medical Research Council Biostatistics Unit, Institute of Public Health, Cambridge, U.K. (http://www.mrc-bsu.cam.ac.uk/bugs).

Toepfer, C.S., Fisher, W.L., and Warde, W.D. 2000. A multistage approach to estimate fish abundance in streams using Geographic Information Systems. N. Am. J. Fish. Manag. **20**: 634–645.

Wyatt, R.J. 2002. Estimating riverine fish population size from single- and multiple-pass removal sampling using a hierarchical model. Can. J. Fish. Aquat. Sci. **59**: 695–706.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics, **12**: 163–189.

© 2003 NRC Canada

Physical constraints on trout (*Oncorhynchus* spp.) distribution in the Cascade Mountains: a comparison of logged and unlogged streams

Joshua J. Latterell, Robert J. Naiman, Brian R. Fransen, and Peter A. Bisson

Abstract: The upstream extent of coastal cutthroat (*Oncorhynchus clarki clarki*) and rainbow (*Oncorhynchus mykiss*) trout distribution in logged and unlogged streams of the western Cascade Mountains appears to be primarily constrained by steep channel gradient and sparse pool habitat. Narrow or intermittent wetted channels are also important constraints in logged drainages. The upstream extent of trout distribution appears to be resilient to the combined impacts of historic and current forest management activities, in the absence of impassable road culverts. The probability of trout presence decreased with channel gradient and increased with pool abundance in both logged and unlogged streams, as indicated by logistic regression analysis of physical stream attributes flanking the trout distribution limit in 37 logged and 21 unlogged streams. Reductions in wetted channel width reduced the likelihood of trout presence in logged streams. Logistic regression models fit to data from logged drainages generated accurate predictions of trout presence or absence when applied to data from unlogged drainages. The pervasive extent of native trout in the channel networks of the Cascade Mountains emphasizes the ecological importance of small streams in watershed planning.

Résumé : La distance en amont à laquelle s'étend la répartition des truites fardées côtières (*Oncorhynchus clarki clarki*) et des truites arc-en-ciel (*Oncorhynchus mykiss*) dans des cours d'eau soumis ou non à la coupe forestière dans la chaîne des Cascades de l'ouest semble être limitée principalement par des chenaux à forte pente et la pénurie d'habitats de profonds. Des chenaux étroits ou immergés de façon intermittente sont aussi des contraintes importantes dans les bassins de drainage exploités. S'il n'y a pas de ponceaux de route impossibles à traverser, l'étendue de la répartition des truites semble résiliente aux impacts combinés des activités de la gestion forestière actuelles et passées. La probabilité de la présence de la truite décroît en fonction de la pente du chenal et augmente avec l'abondance des profonds, tant dans les cours d'eau exploités que dans ceux qui ne le sont pas; c'est ce que révèle une analyse de régression logistique des caractéristiques physiques des cours d'eau en fonction des limites de répartition de la truite dans 37 cours d'eau exploités et 21 qui ne le sont pas. Une diminution de la largeur mouillée du chenal réduit la probabilité de la présence de la truite dans les cours d'eau exploités. Des modèles de régression logistique ajustés aux données provenant de cours d'eau exploités prédisent avec précision la présence ou l'absence des truites lorsqu'on les applique aux données provenant des cours d'eau non exploités. L'étendue remarquable de la répartition de la truite indigène dans les réseaux hydrographiques de la chaîne des Cascades met en relief l'importance écologique des petits ruisseaux dans la planification de la gestion des bassins versants.

[Traduit par la Rédaction]

Introduction

Characterization of habitat features controlling the distribution and abundance of vulnerable fish populations is necessary for effective management of human activities in forested montane watersheds of the Pacific Coastal ecoregion. Despite abundant literature describing the conditions associated with productive trout habitat, the physical conditions associated with the upstream boundary of trout distribution remains poorly known. Similarly, logging-related alterations to physical and biological stream characteristics have been well documented, yet little information exists regarding whether these changes have influenced trout distribution.

Trout distribution has become a key management concern in Washington State because current management regulations restrict certain logging activities along streams where fish are present more than where fish are absent. Trout distribution (i.e., coastal cutthroat (*Oncorhynchus clarki clarki*)

Received 11 June 2002. Accepted 31 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 30 September 2003.
J17173

J.J. Latterell[1] **and R.J. Naiman.** School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, U.S.A.
B.R. Fransen. Weyerhaeuser Company, WTC 1A5, P.O. Box 9777, Federal Way, WA 98063-9777, U.S.A.
P.A. Bisson. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue Southwest, Olympia, WA 98512, U.S.A.

[1]Corresponding author: (e-mail: latterel@u.washington.edu).

 doi: 10.1139/F03-088 © 2003 NRC Canada

and rainbow (*Oncorhynchus mykiss*) trout) is of particular interest because these species typically persist farther upstream than any other fish species in the Cascade Mountains (McPhail 1967; Wydoski and Whitney 1979). Predictive models for mapping trout distribution across landscapes are under development in British Columbia (Porter et al. 2000) and Washington State. Within these efforts, most trout distribution data were collected from streams within commercial forestlands. As a result, uncertainty about whether logging and other related forest management activity have altered the historic boundaries of trout distribution has become an important management concern.

Trout distribution reflects the pattern of colonization and persistence by populations well adapted to modern climatic, biotic, hydrologic, and geomorphic conditions (Nelson et al. 1992). The physical and biotic factors that shape distribution patterns may vary in type and importance over time and space. For example, regional distribution patterns of trout populations near Puget Sound likely reflect the extent of glaciation, arrangement of remnant populations, topography, climate, and dispersal ability (McPhail and Lindsey 1986). Within individual river basins, trout distribution may further reflect variation in temperature (Roper et al. 1994), channel size (Hartman and Gill 1968; Platts 1979) and gradient (Bozek and Hubert 1992; Kruse et al. 1997), species interactions (Fausch et al. 1994), habitat patch size (Reiman and McIntyre 1995), and migratory behavior (Trotter 1989). Within streams and among reaches, dispersal barriers (Nelson et al. 1992; Kruse et al. 1997), catastrophic disturbances (e.g., debris torrents), and spatial variation in factors limiting persistence (e.g., interspecific competition, refugia, nutrient availability, prey abundance, or spawning and rearing habitat) may further regulate trout distribution.

The resilience of trout distribution to forest management activities is difficult to predict because of the wide array of responses exhibited by salmonids to logging-related alterations. Logging influences on salmonid abundance appear to vary according to differences in stream size and the degree to which riparian forest and channel characteristics are modified (Murphy et al. 1986). Potential consequences of contemporary forest management on trout distribution likely depend on the historical harvest practices and the nature of distribution constraints in effect before human disturbance. For example, the historic practice of clearing large woody debris (LWD; diameter ≥10 cm and length ≥2 m) from streams may have diminished fish populations in cleared stream reaches (Dolloff 1986). Without LWD to retain sediments and scour pools, channels that previously exhibited forced step–pool morphology may have reverted to a planebed or bedrock morphology that provides meager "lateral habitat" for trout (Moore and Gregory 1988). Conversely, trout access to headwater stream reaches may actually have been enhanced where management activities removed log jams that obstructed upstream migration (Narver 1971). Likewise, patterns of increased salmonid production after riparian logging have been observed in the Cascade Mountains (Murphy and Hall 1981; Bisson and Sedell 1984), largely as a result of increased autotrophic food pathways. In streams in which bioenergetic demands constrained trout distribution, increased production after logging might facilitate range extension. However, salmonid production may decline shortly after logging, as sunlight is shaded out by dense second-growth canopies (Murphy et al. 1986) and riparian supplies of LWD are exhausted. In streams in which modest or intermittent flows constrain trout distribution, logging-related hydrologic alterations such as increased summer low flows and extension of the open channel (Hicks et al. 1991; Ziemer and Lisle 1998) may enable fish to invade previously inaccessible habitat, at least for a short time. However, as cleared lands revegetate, summer stream flows may actually drop below prelogging levels (Hicks et al. 1991). Debris torrents, which may increase in frequency with forest management (Swanson et al. 1987), can decimate trout populations and dramatically alter channel morphology, though impacted channels appear to be swiftly recolonized (Lamberti et al. 1991).

We sought to determine whether the upstream distribution limits of resident trout occur under similar abiotic conditions in logged and unlogged montane headwater streams draining forested watersheds of the western Cascade Mountains, specifically, have forest management activities enhanced or exacerbated the physical conditions under which trout occur? For example, if steep channel gradients constrain trout distribution, are trout in unlogged watersheds able to invade and persist in steeper streams relative to trout in logged watersheds? We undertook this study to provide a basis for future decision-making in the management of forestry in this region. The objectives of our study were (*i*) to identify the physical constraints and stream characteristics at the upstream limits of trout distribution and (*ii*) to determine whether forest management activities have altered constraints on trout distribution and, consequently, the historic upstream boundaries of trout distribution.

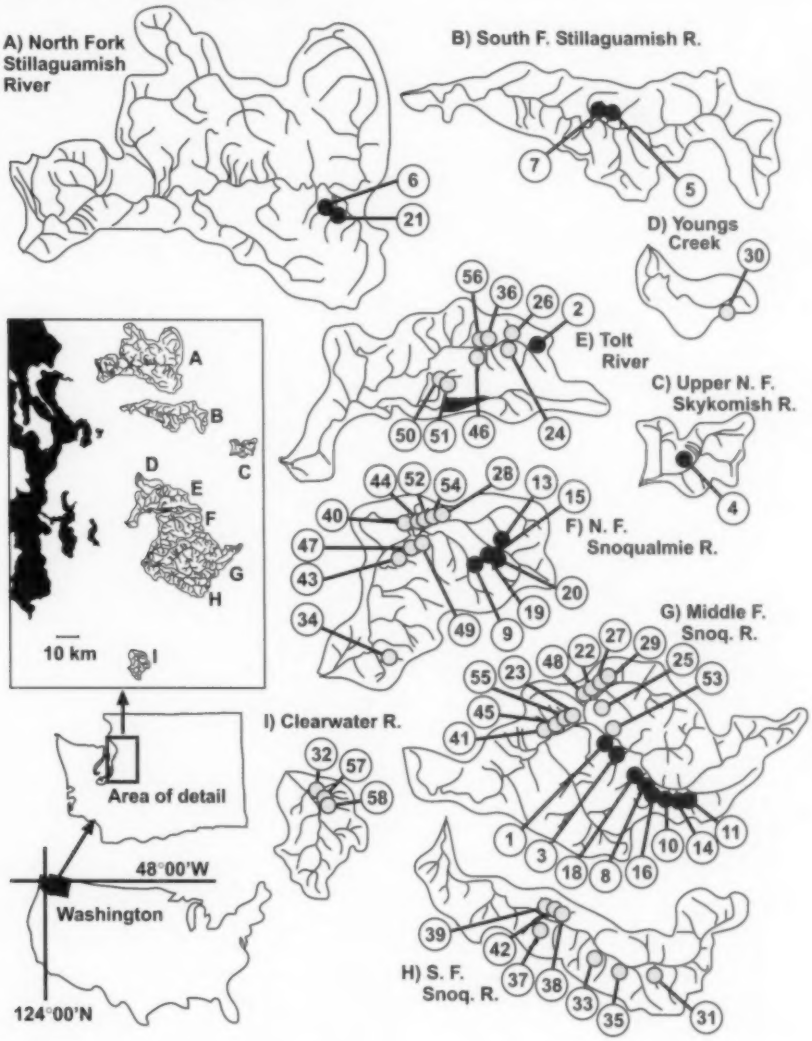
Materials and methods

Study area

The western Cascade Mountain range is located within the northern mainland mountain subregion of the Pacific Coastal ecoregion (Fig. 1), where summers are typically cool and dry and winters are temperate and exceptionally wet (average annual precipitation ranges from 100 to 350 cm). Our study focused on first- and second-order channels that occur within colluvial, bedrock, and small alluvial valleys (Montgomery and Buffington 1998) across a broad range of channel widths (0.5–15 m), gradients (0.1%–50% slope), basin elevations (300–1200 m), and drainage areas (5–1200 ha). Channel substrates are patchy but generally consist of gravels and cobbles. Aquatic vertebrate communities in headwater streams were dominated by coastal cutthroat and rainbow trout, riffle and torrent sculpin (*Cottus gulosus* and *Cottus rhotheus*, respectively), Pacific giant salamander (*Dicamptodon tenebrosus*), and tailed frogs (*Ascaphus truei*). Natural disturbances strongly shape headwater stream ecology and structural characteristics. Rapid snowmelt or "rain-on-snow" events drive peak stream flows in the spring and early summer. Headwater stream channels may run dry before fall rains or be sustained throughout the summer by late-melting snow, depending on elevation (Ziemer and Lisle 1998). Swift flood surges laden with woody debris, alluvium, and soil (debris flows) occasionally restructure channel morphology and riparian forest structure (Swanson et al.

© 2003 NRC Canada

Fig. 1. Map of study sites in the Cascade Mountains, Washington. Spatial juxtaposition of subbasins (i.e., A–I) is illustrated in the "Area of detail". Locations of numbered study sites are indicated by circles on the enlarged subbasin diagrams. Solid circles indicate unlogged sites and shaded circles indicate logged sites.



1987). Autochthonous production in small headwater streams is typically low (Naiman and Sedell 1979), limited by low nutrient availability, cold temperatures, and dense riparian canopies (Murphy et al. 1981) of western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*).

Study design

A paired-reach sampling design was used to assess the influence of physical habitat attributes on the likelihood of trout presence and absence in 58 separate low-order streams (Fig. 1). Streams draining lakes, ponds, or hanging valleys were excluded because many have been artificially populated with hatchery-raised trout or exotic species. Field surveys were conducted in 1999 and 2000 between the late-spring snowmelt runoff and summer low-flow periods (May–September). Detailed habitat inventories were conducted in two contiguous 100-m sections immediately upstream and downstream of the upper distribution limit (i.e., the last trout observed).

Sites from both unlogged (N = 21) and logged (N = 37) drainages were surveyed to determine whether the likelihood of trout presence and absence in streams of similar physical character differed between drainages managed for timber production and protected drainages representative of pre-logging conditions. Most of the drainage area upstream from unlogged sites remained in native late-seral forest, whereas most trees had been harvested at least once in logged sites. At logged sites, riparian forests had been clearcut once or twice in the past, though contemporary harvests left intact streamside forest buffers. Time elapsed since last harvest ranged widely across logged sites, from <2 years (e.g., recently harvested) to ~50 years (e.g., second growth). Gen-

© 2003 NRC Canada

erally, a suite of forest management activities occurred at logged sites, most notably road construction and culvert installation.

Data collection

A single electrofishing pass was used to locate the upstream limit of trout distribution. Sampling was initiated in a trout-bearing stream reach and progressed upstream until one of the following minimum criteria was met: (*i*) no trout were encountered for 400 m, despite rigorous searching, (*ii*) the channel was dry for over 200 m, or (*iii*) upstream channel slope consistently exceeded 30%. Sampling often continued beyond the point where these minimum criteria were met whenever the surveyor's confidence in the identified distribution limit was in doubt.

Habitat characteristics, including (*a*) mean channel gradient, (*b*) bankfull and wetted channel width, (*c*) pool characteristics, (*d*) LWD abundance, and (*e*) canopy closure, were measured in 100-m (slope distance) stream reaches immediately upstream and downstream from the trout distribution limit. Channel gradient (% slope) was measured incrementally over segments of uniform gradient but variable length, using a clinometer. Horizontal distance and elevation gain were calculated for each segment. Mean channel gradient for each 100-m section was calculated by dividing the total elevation gain by the total horizontal distance over all individually measured segments. Wetted (WW) and bankfull channel widths (BFW), as indicated by bank shape and perennial vegetation, were measured with a fiberglass tape to the nearest 0.1 m at transects spaced 20 m apart perpendicular to flow and were averaged for each section. To improve survey consistency across streams of different sizes, slow-water habitats were only considered pools if minimum criteria were met. Residual pool depth had to meet or exceed 0.1 m, whereas minimum pool area was scaled to BFW. Specifically, only pools ≥0.5 m^2 in area (as per visual estimation) were counted where mean BFW was 0–2.5 m. Likewise, the minimum pool area was 1, 2, and 3 m^2 where BFW was 2.5–5, 5–10, and 10–15 m, respectively (adapted from 1994 Timber–Fish–Wildlife Ambient Monitoring Program Manual, Northwest Indian Fisheries Commission, 6730 Martin Way East, Olympia, WA 98506, U.S.A.). Pools that met these criteria were tallied and measured for residual depth (Lisle 1987) in all streams. Features contributing to pool formation were recorded for each pool. Pieces of LWD intruding into the wetted channel were tallied for each section at every site. The general condition of riparian and surrounding forests was qualitatively assessed (e.g., young, pole, mature, and old), according to tree stem diameter and vertical complexity of the stand. A spherical densiometer was used to estimate canopy closure (%) at each transect. A digital altimeter was used to determine the elevation at each distribution limit. The geographic location of each distribution limit was recorded on 1 : 24 000 topographic maps and transferred into a geographic information system (GIS). Drainage area at each distribution limit was estimated with ArcInfo™ 8.0 (ESRI, Inc., 380 New York St., Redlands, CA 92373-8100) from 10-m digital elevation models derived by the University of Washington Puget Sound Regional Synthesis Model (PRISM) working group.

Data analysis

Logistic regression was used to model the likelihood of trout presence in a 100-m stream reach as a function of physical stream attributes in all sites combined (i.e., full combined model, A), logged sites (i.e., full logged model, B), and unlogged sites (i.e., full unlogged model, C). Models were fitted without interactions, as recommended by Neter et al. (1996), to permit the interpretation of $\exp(\beta_a)$ as the odds ratio. All analyses were performed with SPSS 10.0.5 (SPSS Inc. 1989–1999). Logistic regression provided a probabilistic prediction of trout presence and was well suited for this application because the dependent variable was binomial (trout presence or absence). Further, this technique does not assume normality, equal variances, or a linear response (Tabachnick and Fidell 1996). The form of the fitted multiple logistic regression model or response function is

$$(1) \qquad \pi = e^{\beta' X}/(1 + e^{\beta' X})$$

where π is the estimated probability of trout presence, and $\beta' X$ is the linear model, which is

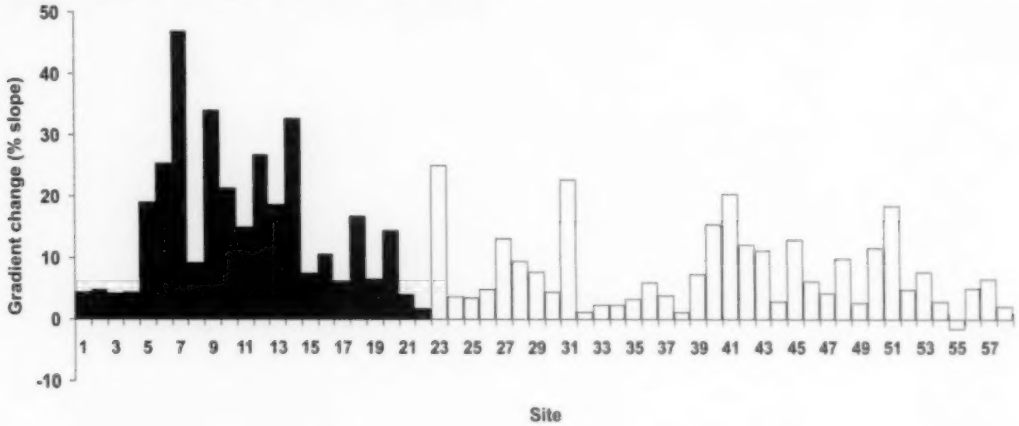
$$(2) \qquad \beta' X = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_a X_a$$

where β_0 is the regression constant, β_a denote regression coefficients, and X_a denote independent predictor variables. As indicated above, logistic regression calculates the probability of success (i.e., trout presence, $\pi \geq 0.50$) over the probability of failure (i.e., trout absence, $\pi < 0.50$), which results in an estimated odds ratio, $\exp(\beta_a)$. The effect of increasing one predictor variable X_a by a single unit on the odds of trout presence is estimated by multiplying the probability of trout presence by $\exp(\beta_a)$, assuming that all other predictor variables are held constant (Neter et al. 1996). Stream attributes that differed between reaches upstream and downstream of the trout distribution limit ($p \leq 0.05$, Wilcoxon signed ranks tests) or between logged and unlogged sites ($p \leq 0.05$, Mann–Whitney *U* tests) were eligible for inclusion in the logistic regression models. Attributes with strong multicollinearity ($|r_S| \geq 0.50$) were excluded to improve the descriptive and predictive ability of the models (Neter et al. 1996). The Wald statistic was used to evaluate the statistical significance of the influence of each stream attribute on the likelihood of trout occurrence. Log-likelihood tests were used to determine which variables could be removed from the model. Chi-square goodness-of-fit (i.e., model χ^2) tests were used to determine whether the set of stream attributes was significantly related to the likelihood of trout presence. The probability of trout presence for each stream section was predicted from stream attributes and compared with the observed trout occurrence to assess model performance.

A simple model using channel gradient as the only predictor variable was also fit to the entire data set (i.e., combined gradient model, A_G) and separately to data from logged (i.e., logged gradient model, B_G) and unlogged sites (i.e., unlogged gradient model, C_G) to determine whether the likelihood of trout presence could be accurately predicted from channel gradient alone, as observed for Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) (Kruse et al. 1997). Accurate predictive tools based on gradient alone have strong management utility, because channel gradient is easily approximated from topographic maps or digital eleva-

© 2003 NRC Canada

Fig. 2. Change in channel gradient encountered by trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) at the upstream limit of distribution at unlogged (solid bars) and logged (open bars) sites.

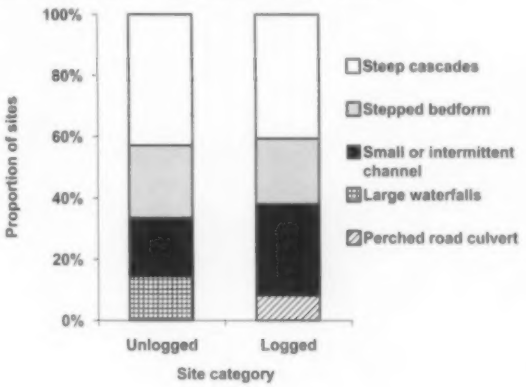


tion models and because stream characteristics, such as pool spacing and depth and channel width, are often related to channel gradient, as mediated by LWD (Montgomery and Buffington 1998).

Separate multiple logistic regression models (B, B_G, C, and C_G) were fitted to data from logged sites and unlogged sites and cross-validated to determine whether logging and related forest management activity have altered historic upstream boundaries of trout distribution. Comparison of the models indicates whether similar abiotic factors determine upstream distribution limits in logged and unlogged streams selected for study, though we cannot discern whether these models have general applicability to other watersheds in the region. The preferred method for validation of regression models is through the collection of new data from other watersheds in the region, though this was not feasible. In the absence of new data collected from other watersheds in the region, cross-validation is useful in evaluating the reasonableness and predictive ability of the selected model (Neter et al. 1996), in this case, the performance of a model based on data from logged streams when applied to unlogged streams is of primary interest.

In cross-validation, data sets from logged sites and unlogged sites were used alternately as "model-building" and "validation" sets (Neter et al. 1996). Models were applied to validation data sets (i.e., full logged model B vs. unlogged sites data set and full unlogged model C vs. logged sites data set). The probability of trout presence for each stream section was predicted from habitat features in the validation data set and compared with the observed trout presence. Cohen's kappa (K) values (Cohen 1960) were used to interpret the classification results of each logistic model, as recommended by Titus and Mosher (1984). The K statistic indicates whether model predictions are significantly better than random classifications; it expressed the proportion of sites correctly classified by the model after removing the effect of correct classification by chance. When $K = 0$, no improvement over chance was provided by the logistic regression model, whereas $K = 1$ only when all cases are correctly classified. When K is much lower than the observed correct classification rate, the observed classification rate and, subsequently, group predictability are overstated. The statistical significance of kappa values were assessed with the z statistic, as recommended by Titus and Mosher (1984).

Fig. 3. General features of reaches immediately upstream from the trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) distribution limit at unlogged and logged sites.



Results

Stream attributes of the upstream distribution limit

The upstream limit of trout distribution was frequently associated with a sharp increase in channel gradient (Fig. 2). Steep cascades, stepped-bed channel profiles, or waterfalls appeared to restrict upstream dispersal in a majority of logged (62.2%) and unlogged sites (81.0%) (Fig. 3). Channel gradient was significantly greater in stream reaches where trout were absent in both unlogged and logged sites ($p < 0.01$; Wilcoxon signed ranks test) (Table 1). Mean channel gradients in the downstream reaches of unlogged and logged sites averaged 9.1% but ranged from 1% to 22% overall. Trout were consistently absent from channels where gradient exceeded 22%, despite intensive surveys in channels up to 53% gradient. The mean channel gradient of reaches where trout were absent was greater ($p < 0.01$) in unlogged sites, as

© 2003 NRC Canada

Table 1. Key stream habitat characteristics for 100-m stream reaches immediately upstream (U) and downstream (D) of the upstream limit of trout distribution in unlogged and logged sites and all sites combined.

		Unlogged			Logged			Combined		
Stream characteristic	Statistic	U		D	U		D	U		D
Channel gradient (%)	Mean (SE)	25.0* (2.6)	>	9.1 (1.0)	16.7* (1.2)	>	9.1 (0.8)	19.7 (1.3)	>	
	Range	7–53		3–21	6–37		1–22	6–53		1–22
Bankfull width (m)	Mean (SE)	6.4 (0.6)	=	5.7 (0.7)	5.4 (0.5)	=	5.5 (0.5)	5.7 (0.4)	=	5.5 (0.4)
	Range	2–13		2–16	2–16		2–16	2–16		2–16
Wetted width (m)	Mean (SE)	3.8* (0.5)	=	3.5 (0.5)	2.2* (0.3)	<	2.8 (0.2)	2.8 (0.3)	=	3.1 (0.2)
	Range	0–8		1–11	0–6		1–6	0–8		1–11
No. pools·100 m^{-1}	Mean (SE)	13.1 (1.8)	<	17.1 (1.8)	12.2 (1.6)	<	15.5 (1.5)	12.5 (1.2)	<	16.1 (0.2)
	Range	0–28		2–30	0–31		0–33	0–31		0–33
Residual pool depth (cm)	Mean (SE)	24.9 (3.3)	=	30.2 (6.6)	26.2 (2.8)	=	25.7 (1.8)	25.7 (2.1)	=	27.3 (2.7)
	Range	10–77		12–158	11–89		12–54	10–89		10–158
LWD·100 m^{-1}	Mean (SE)	41.9 (5.6)	=	42.1 (6.1)	48.8 (5.7)	=	40.2 (4.6)	46.3 (4.1)	=	40.9 (3.6)
	Range	0–85		9–139	5–159		0–106	0–159		0–159
Gravel substrate (%)	Mean (SE)	14.9* (2.8)	<	25.6 (3.8)	28.3* (4.2)	=	26.5 (2.8)	22.4 (2.8)	=	26.1 (2.2)
	Range	0–40		7–73	0–84		0–63	0–84		0–84
Canopy closure (%)	Mean (SE)	73.3 (6.0)	=	72.6 (5.4)	70.2 (4.3)	=	71.3 (4.4)	71.3 (3.5)	=	71.8 (3.4)
	Range	4–100		12–100	17–100		18–100	4–100		12–100

Note: Asterisks (*) indicate where significant differences ($p \leq 0.05$, Mann–Whitney U test) exist between unlogged and logged sites (e.g., unlogged U vs. logged U). Differences ($p \leq 0.05$, Wilcoxon signed ranks test) between U and D sections are indicated with "<" or ">" according to the direction of the differences or by "=" if no difference was detected. SE, standard error; LWD, large woody debris.

indicated by Mann–Whitney *U* tests (Table 1). Gradient immediately upstream of the limit of trout distribution in unlogged sites averaged 25.0% vs. 16.7% in logged sites. Waterfalls were associated with the upstream trout distribution limit in 3 of 21 (14.3%) unlogged sites (Fig. 3).

The limit of trout distribution was typically associated with declines in pool abundance in both unlogged and logged sites (Fig. 4). Pool abundance was significantly lower in stream reaches where trout were absent ($p < 0.01$, Wilcoxon signed ranks tests; Table 1), though few of these were completely devoid of pools (i.e., four logged sites and one unlogged site). Trout were found in reaches without pools at only one site. Pool abundance averaged 16·100 m^{-1} in downstream reaches and 13·100 m^{-1} in upstream reaches, most of which were formed by scour around boulders and woody debris. Pool abundance was similar in unlogged and logged sites, as indicated by Mann–Whitney *U* tests (Table 1). In several streams, isolated pools bounded by dry streambed comprised the only habitat available at the upstream limit of trout distribution; trout crowded into these pools at high densities (i.e., >5 individuals·m^{-2}).

Channel constrictions or subsurface flows were associated with the upstream limit of trout distribution more frequently in logged sites than in unlogged sites (Fig. 3). The wetted width of upstream reaches was usually narrower than that of the downstream reaches in logged sites (Fig. 5). In contrast, wetted channel width did not differ between upstream and downstream reaches in unlogged sites (Table 1). Mean wetted widths of upstream reaches were significantly narrower ($p \leq 0.01$) in logged sites than in unlogged sites (Table 1). Wetted channel widths in downstream sections of unlogged and logged sites were indistinguishable ($p > 0.05$). Trout were found in isolated pools upstream from the initiation point of perennial streamflow at three sites, but never where the mean wetted channel width averaged less than 0.3 m·100 m^{-1}. In unlogged sites, substrates were significantly coarser in upstream reaches, though the relative proportion of substrate classes was strongly correlated with channel gradient.

Other habitat characteristics, including bankfull width, residual pool depth, number of LWD, and canopy closure, did not differ among upstream and downstream sections or between unlogged and logged sites. Drainage area, elevation, and mean annual precipitation at the distribution limit varied widely but did not differ significantly between unlogged and logged sites. Drainage area at the upstream limit of distribution averaged 130 ha across all sites and ranged from 2 to 517 ha. Elevation at the upstream limit of trout distribution ranged from 279 to 962 m. Forest stands were classified as young, pole, and mature in 18.9, 73.0, and 8.1%, respectively, of logged sites. Stands were classified as young, pole, mature, and old in 9.5, 14.3, 23.8, and 52.4%, respectively, of the unlogged sites.

Relationship between trout presence and physical stream attributes

The likelihood of trout presence declined with increasing channel gradient, decreased pool abundance, and decreased wetted channel width across all sites combined (Table 2), though trout presence was not related to wetted channel width in unlogged sites. Other variables were either not significantly related to trout presence and absence or were ex-

© 2003 NRC Canada

Fig. 4. Change in pool frequency (per 100 m) encountered by trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) at the upstream limit of distribution at unlogged (solid bars) and logged (open bars) sites.

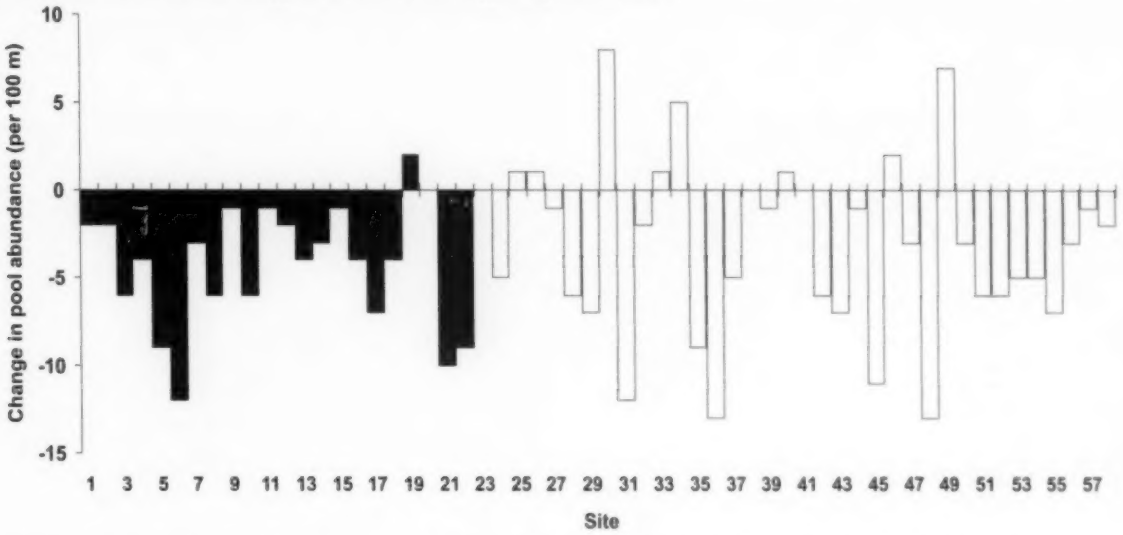
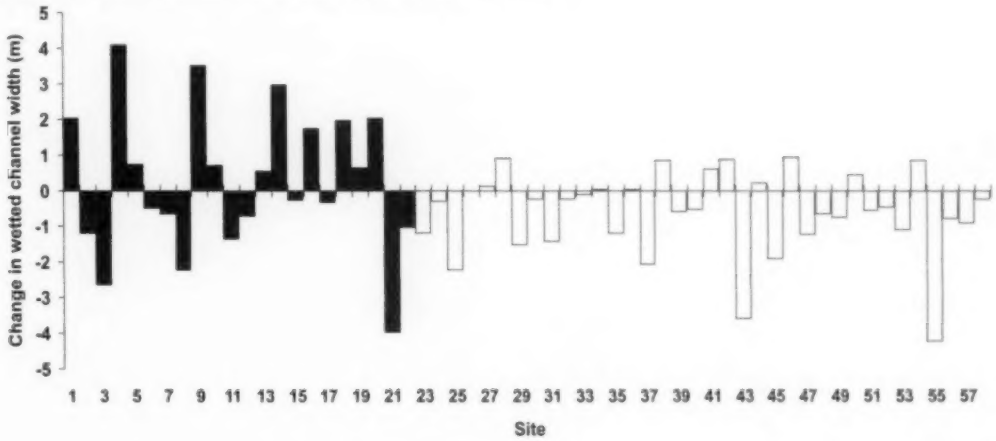


Fig. 5. Change in wetted channel width encountered by trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) at the upstream limit of distribution at unlogged (solid bars) and logged (open bars) sites.



cluded because of strong multicollinarity ($r_S \geq 0.50$). Chi-square goodness-of-fit tests indicated that the logistic response function was appropriate for all models. The full combined model (A) fitted to all sites correctly classified trout presence or absence in 100 of 116 (86.2%) stream reaches. Fifty-two of 58 stream reaches (89.7%) were correctly classified as trout bearing, and 48 of 58 stream reaches (82.8%) were correctly classified as devoid of trout. The chance-corrected classification rate (K = 72.4% ± 12, 95% confidence interval (CI)) was significantly better ($p < 0.01$) than would be expected resulting from chance alone. Assuming other variables were held constant, model A indicated that a 1% increase in channel gradient (e.g., 11% to 12%) reduced the odds of trout presence by 29%–32%. Likewise, the presence of one additional pool per 100-m stream section, assuming other predictor variables were held constant, increased the odds of trout presence by 12%–18%. Increasing wetted channel width by 1 m increased the odds of trout presence by 182%, assuming other predictor variables were held constant. The combined gradient model (A_G) correctly classified trout presence or absence in 84 of 116 (72.4%) stream reaches, overall. The chance-corrected classification rate (K = 44.8% ± 17, 95% CI) indicated that this model correctly classified more stream reaches than would be expected resulting from chance alone ($p < 0.01$).

Autocorrelations were observed among each factor included in the logistic regression models, but factors were retained if we considered them to represent unique mechanistic controls on trout distribution so long as $|r_S|$ did not exceed 0.50. Channel gradient was correlated with wetted channel width in both upstream (r_S = 0.33, $p < 0.05$) and downstream (r_S = 0.45, $p < 0.05$) sections but was only correlated with pool

© 2003 NRC Canada

Table 2. Logistic regression analysis results for models of the relationship between the likelihood of trout presence and physical stream attributes, based on data from all sites combined, logged sites, and unlogged sites, and the associated change in odds of fish presence resulting from a one-unit increase in the stream attribute, controlling for other attributes.

Data set	*N*	Model	Variables	*b* (SE)	*p*	Exp(*b*) (95% CI)	Change in odds (%)
Combined	116	A	Constant	0.961 (0.719)	0.18		
			Gradient	–0.335 (0.065)	<0.01	0.715 (0.630–0.812)	–29.5
			Wetted width	0.560 (0.197)	0.01	1.750 (1.189–2.576)	+75.0
			Pool abundance	0.114 (0.036)	<0.01	1.121 (1.045–1.203)	+12.1
		A_G	Constant	2.765 (0.559)	<0.01		
			Gradient	–0.209 (0.041)	<0.01	0.812 (0.746–0.880)	–18.8
Logged	74	B	Constant	0.553 (0.927)	0.55		
			Channel gradient	–0.389 (0.092)	<0.01	0.678 (0.566–0.811)	–32.2
			Wetted width	1.037 (0.315)	<0.01	2.820 (1.520–5.232)	+182.0
			Pool abundance	0.096 (0.044)	0.03	1.101 (1.010–1.200)	+10.1
		B_G	Constant	2.397 (0.659)	<0.01		
			Channel gradient	–0.192 (0.050)	<0.01	0.825 (0.748–0.910)	–17.5
Unlogged	42	C	Constant	2.264 (1.232)	0.07		
			Channel gradient	–0.340 (0.104)	<0.01	0.712 (0.581–0.873)	–28.8
			Pool abundance	0.168 (0.076)	0.03	1.183 (1.020–1.374)	+18.3
		C_G	Constant	3.619 (1.073)	<0.01		
			Channel gradient	–0.244 (0.074)	<0.01	0.783 (0.677–0.906)	–21.7

Note: SE, standard error; CI, confidence interval.

abundance in downstream sections (r_S = 0.47, $p < 0.05$). Wetted channel width and pool abundance were correlated in upstream sections alone (r_S = 0.28, $p < 0.05$), whereas wetted channel width and residual pool depth were correlated in upstream (r_S = 0.38, $p < 0.05$) and downstream (r_S = 0.46, $p < 0.05$) sections.

Comparison of trout distribution in logged and unlogged streams

Separate models fitted to logged (B, B_G) and unlogged (C, C_G) sites performed fairly well when applied to validation data sets; each model correctly predicted trout presence or absence in over 70% of the stream sections in the validation sets (Table 3). Kappa values were relatively high (43–71%; Table 3), indicating that each model correctly predicted trout presence and absence in a much greater proportion of the stream reaches than would be expected from chance alone. However, all *K* values were slightly lower than the observed correct classification rate, which suggests that uncorrected model performance may have been slightly overstated. The probability of trout presence declined with increasing channel gradient and decreasing pool abundance at both logged and unlogged sites, though wetted channel width was only related to trout presence at logged sites. The full unlogged model (C) predicted trout presence where trout were actually absent in 14 of 37 (38%) logged stream reaches, whereas the full logged model (B) predicted trout presence where trout were actually absent for only 4 of 21 (19.0%) unlogged stream reaches. The full logged model (B) correctly predicted trout presence and absence in slightly more of the unlogged stream reaches than the logged gradient model (B_G). The models based on unlogged sites (C, C_G) were equally successful, overall, in predicting trout presence and absence in logged stream reaches.

Discussion

Physical constraints on trout distribution

Our results indicate that the upstream boundaries of coastal cutthroat and rainbow trout distribution in low-order streams of the western Cascade Mountains near Puget Sound are influenced by steep channel gradient, the availability of pool habitat, and small stream size. Although this study examined only 58 streams, we believe that these factors have strong effects on the extent of trout distribution in many headwater streams of the Cascade Mountains. The probability of trout presence significantly decreased in steeper channels but increased with increasing stream size and pool abundance. The influence of channel gradient appeared to overwhelm the effects of either pool abundance or wetted width, though autocorrelation among channel gradient, pool abundance, and wetted channel width precludes inferences on the relative importance of each factor. Trout readily accessed channels with up to a 22% gradient and commonly occurred where channel gradient exceeded 10%. Similar ranges have been reported for Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*; Dunham et al. 1999) and bull trout (*Salvelinus confluentus*; Watson and Hillman 1997). Based on our results, trout were more likely to be present in steep channels when pool habitat was plentiful. Pools probably facilitated trout access and persistence in steep channels by providing

© 2003 NRC Canada

Table 3. Proportion of stream reaches where trout presence was correctly classified in cross-validation tests (i.e., models B and B_G were used to classify unlogged stream reaches, and models C and C_G were used to classify logged stream reaches).

		Unlogged stream reaches		Logged stream reaches	
		Model B	Model B_G	Model C	Model C_G
Trout present	Predicted	19	18	30	31
	Actual	21	21	37	37
	Correct	0.905	0.857	0.811	0.838
Trout absent	Predicted	17	17	23	22
	Actual	21	21	37	37
	Correct	0.810	0.810	0.622	0.595
Overall	Correct	0.857	0.833	0.716	0.716
Chance-corrected	Kappa (95% CI)	0.714 (0.22)	0.666 (0.23)	0.432 (0.20)	0.432 (0.21)
	p	<0.01	<0.01	<0.01	<0.01

Note: CI, confidence interval.

launching areas for leaping barriers (Adams et al. 2000) and refugia from predation and thermal extremes during summer low flows (Bisson et al. 1988). Stream size has been identified as a driving factor in the presence and abundance of stream salmonids (e.g., coastal cutthroat trout) elsewhere in the ecoregion (Rosenfeld et al. 2000). Our data indicate that trout were less likely to occur as the wetted channel became negligible or intermittent, though our observations indicate that the extreme margins of trout distribution may extend beyond the point at which streams exhibit seasonal intermittency. Other variables examined in this study did not appear to be important constraints on the upstream trout distribution limits in the streams that we examined.

The stability of the upstream limit of trout distribution over space and time remains ripe for future research. Stream salmonids may exhibit extensive, complex patterns of movement, though the mechanisms determining the frequency and extent of movement remain poorly understood (Gowan et al. 1994). The steep, narrow stream reaches that epitomize the upstream distribution limit of trout may be volatile and heterogeneous over time. Assuming that at least a small number of individuals in a trout population exhibit extensive movements (see Gowan and Fausch 1996), we speculate that fluctuations in upstream distribution limits, in concert with variation in habitat suitability and accessibility, are likely.

Influence of logging on trout distribution

Although logging and related activities may influence the structural and biotic attributes of headwater streams (Murphy and Hall 1981; Bisson and Sedell 1984; Gregory et al. 1987), the combined impacts of historic and current forest management activity within low-order streams of the Cascade Mountains near Puget Sound do not appear to have altered the conditions under which the upper boundary of trout distribution occurs. Trout presence and absence in unlogged streams was predicted with a high degree of accuracy by the logistic regression model based on stream attributes near the distribution limit of trout in logged streams. However, though geomorphic habitat characteristics were similar between unlogged and previously logged streams in the downstream section where trout were present, the gradient and wetted channel width upstream from the upper distribution limit were greater, on average, in unlogged sites. Observed differences in stream attributes above the upper distribution limit may have been caused by rather abrupt increases in channel gradient at some unlogged sites in watersheds with steep valley walls. Trout appear to inhabit streams with similar attributes in logged and unlogged sites but are unlikely to access and persist in streams once channel gradient, pool abundance, or wetted channel widths exceed certain thresholds. The high degree of success exhibited by cross-validation of the full logged model (B) on the unlogged data set suggests that these thresholds occur at similar levels in logged and unlogged sites.

Logging and related activities may alter key factors that regulate small-scale channel gradient, or bed slope, such as sediment supply, transport capacity, and the vegetation within and adjacent to the channel (Montgomery and Buffington 1998). Increased discharge may trigger channel incision, whereas aggradation may occur in streams with exhausted transport capacity. Channel gradient at the reach scale (e.g., ≥100 m) may be relatively resilient to logging-related impacts because it is largely controlled by large-scale processes such as tectonic uplift and erosion of the landscape over geologic time (Montgomery and Buffington 1998).

In conclusion, habitat-based models are valuable tools for estimating upstream distribution limits of trout, particularly in areas where intrusive field surveys are unadvisable, such as those inhabited by threatened or endangered fish populations. Our results indicate that easily measured channel features can be used to accurately predict the incidence of trout in streams during late spring and summer. Because the extent of trout distribution throughout entire river basins may be governed by factors operating at other spatial scales (see Huryn and Wallace 1987), our models should be used in conjunction with detailed surveys of large waterfalls or other known barriers when predicting the upstream extent of trout distribution. Application of our models in regions with fundamentally different hydrologic, erosional, or tectonic processes is not advised because relationships between trout distribution and channel morphology probably differ among watersheds in different biogeographic or geomorphic provinces (Nelson et al. 1992; Montgomery and Buffington 1998; Hicks and Hall 2003).

Our investigation considered the influence of major physical factors on patterns of reach-scale trout distribution, but

© 2003 NRC Canada

patterns at larger scales (e.g., segment, valley, and watershed) may also reflect biotic processes. The ability of trout to invade and persist in steep streams may also be regulated, in part, by biotic factors such as predation or intraspecific competition for food and refugia. Further investigations are warranted for a more comprehensive understanding of the factors responsible for patterns of trout distribution within and among streams.

Our results highlight the prevalence and resiliency of native trout in very small, steep streams of forested mountain watersheds in the Cascade Mountains. Historically, small headwater streams of the Pacific Coastal ecoregion have received little protection from land-management actions because it was incorrectly believed that they contained few or no fish, despite their broader ecological significance. Only recently have headwater streams benefited from increased protection from potentially damaging land-use practices. Population characteristics of stream-resident trout in the Pacific Coastal ecoregion remain poorly known. The distribution patterns of stream-dwelling trout appear relatively resilient to anthropogenic and natural disturbances. However, connectivity between trout populations in small, headwater streams may be necessary for the long-term maintenance of genetic (and presumably adaptive) diversity (Latterell 2001) and to permit recolonization following stochastic extinctions of local populations resulting from natural metapopulation dynamics. Reducing or eliminating unnatural barriers to upstream dispersal (such as suspended culverts) is needed to ensure that the natural distribution potential and patterns of gene flow in trout populations is fully realized.

Acknowledgements

We thank Robert E. Bilby and Thomas C. O'Keefe for intellectual contributions and thoughtful discussions that enhanced the study. We gratefully acknowledge comments from David Beauchamp, Robert E. Bilby, Brendan J. Hicks, and Carter Kruse, which improved the manuscript. Field assistance was provided by Nick Hurtado and Jennifer Bahrke. Guy McWethy performed geospatial analyses, and Miles Logsdon and Harvey Greenberg assisted with PRISM-related data. Statistical advice was provided by Loveday Conquest. Funding for this project was contributed by the U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Weyerhaeuser Company, the University of Washington Puget Sound Regional Synthesis Model (PRISM) project, and the University of Washington Center for Water and Watershed Studies (formerly the Center for Streamside Studies).

References

Adams, S.B., Frissell, C.A., and Rieman, B.E. 2000. Movements of nonnative brook trout in relation to stream channel slope. Trans. Am. Fish. Soc. **129**: 623–638.

Bisson, P.A., and Sedell, J.R. 1984. Salmonid populations in clear-cut vs. old-growth forests of western Washington. *In* Fish and wildlife relationships in old-growth forests: Proceedings of a symposium. *Edited by* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley. Am. Inst. Fish. Biol., Morehead City, N.C. pp. 121–129.

Bisson, P.A., Sullivan, K., and Nielsen, J.L. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout. Trans. Am. Fish. Soc. **117**: 262–273.

Bozek, M.A., and Hubert, W.A. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Can. J. Zool. **70**: 886–890.

Cohen, J. 1960. Weighted kappa: nominal scale agreement with provisions for scaled disagreement or partial credit. Psychol. Bull. **70**: 213–220.

Dolloff, C.A. 1986. Effects of stream clearing on juvenile coho salmon and Dolly Varden in Southeast Alaska. Trans. Am. Fish. Soc. **125**: 743–755.

Dunham, J.B., Peacock, M.M., Reiman, B.E., Schroeter, R.E., and Vinyard, G.L. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Trans. Am. Fish. Soc. **128**: 875–889.

Fausch, K.D., Nakano, S., and Ishigaki, K. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia, **100**: 1–12.

Gowan, C., and Fausch, K.D. 1996. Mobile brook trout in two high elevation Colorado streams: re-evaluating the concept of restricted movement. Can. J. Fish. Aquat. Sci. **53**: 1370–1381.

Gowan, C., Young, M.K., Fausch, K.D., and Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can. J. Fish. Aquat. Sci. **51**: 2626–2637.

Gregory, S.V., Lamberti, G.A., Erman, D.C., Koski, K.V., Murphy, M.L., and Sedell, J.R. 1987. Influence of forest practices on aquatic production. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. Institute of Forest Research, University of Washington, Seattle, Wash. pp. 233–256.

Hartman, G.F., and Gill, C.A. 1968. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. J. Fish. Res. Board Can. **25**: 33–48.

Hicks, B.J., and Hall, J.D. 2003. Rock type and channel gradient structure salmonid populations in the Oregon Coast Range. Trans. Am. Fish. Soc. **132**: 468–482.

Hicks, B.J., Hall, J.D., Bisson, P.A., and Sedell, J.R. 1991. Response of salmonid populations to habitat changes caused by timber harvest. *In* Influence of forest and rangeland management on salmonid fishes and their habitats. *Edited by* W.D. Meehan. Am. Fish. Soc. Spec. Pub. No. 19, Bethesda, Md. pp. 483–518.

Huryn, A.D., and Wallace, J.B. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology, **68**: 1932–1942.

Kruse, C.G., Hubert, W.A., and Rahel, F.J. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. Trans. Am. Fish. Soc. **126**: 418–427.

Lamberti, G.A., Gregory, S.V., Ashkenas, L.R., Wildman, R.C., and Moore, K.M.S. 1991. Stream ecosystem recovery following a catastrophic debris flow. Can. J. Fish. Aquat. Sci. **48**: 196–208.

Latterell, J.J. 2001. Distribution constraints and population genetics of native trout in unlogged and clear-cut headwater streams. M.S. Thesis, University of Washington, Seattle.

Lisle, T.E. 1987. Using "residual depths" to monitor pool depths independently of discharge. U.S. Department of Agriculture Forest Service, Berkley, Calif. Res. Note PSW-394,

McPhail, J.D. 1967. Distribution of freshwater fishes in Western Washington. Northw. Sci. **41**: 1–11.

McPhail, J.D., and Lindsey, C.C. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia systems and rivers north to the Stikine). *In* The zoogeography of North American fresh-

© 2003 NRC Canada

water fishes. *Edited by* C.H. Hocutt and E.O. Wiley. John Wiley & Sons, New York. pp. 615–637.

Montgomery, D.R., and Buffington, J.M. 1998. Channel processes, classification, and response. *In* River ecology and management: lessons from the Pacific coastal ecoregion. *Edited by* R.J. Naiman and R.E. Bilby. Springer-Verlag New York, Inc., New York. pp. 13–42.

Moore, K.M.S., and Gregory, S.V. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade mountain streams. Can. J. Fish. Aquat. Sci. **117**: 162–170.

Murphy, M.L., and Hall, J.D. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade mountains, Oregon. Can. J. Fish. Aquat. Sci. **38**: 137–145.

Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. **110**: 469–478.

Murphy, M.L., Hefietz, J., Johnson, S.W., Koski, K.V., and Thedinga, J.F. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Can. J. Fish. Aquat. Sci. **43**:1521–1533.

Naiman, R.J., and Sedell, J.R. 1979. Benthic organic matter as a function of stream order in Oregon. Arch. Hydrobiol. **87**: 404–422.

Narver, D.W. 1971. Effects of logging debris on fish production. *In* Forest land uses and stream environment: Proceedings of a symposium. *Edited by* J.T. Krygier and J.D. Hall. Oregon State University, Corvallis, Oreg. pp. 100–111.

Nelson, R.L., Platts, W.S., Larsen, D.P., and Jensen, S.E. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, Northeastern Nevada. Trans. Am. Fish. Soc. **121**: 405–426.

Neter, J., Kutner, M.H., Nachtsheim, C.J., and Wasserman, W. 1996. Applied linear regression models. 3rd ed. The McGraw-Hill Companies, Inc., Chicago, Ill.

Platts, W.S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries, **4**: 5–9.

Porter, M., Rosenfeld, J., and Parkinson, E. 2000. Predictive models of fish species distribution in the Blackwater Drainage, British Columbia. N. Am. J. Fish. Manag. **20**: 349–359.

Reiman, B.E., and McIntyre, J.D. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Trans. Am. Fish. Soc. **124**: 285–296.

Roper, B.B., Scarnecchia, D.L., and La Marr, T.J. 1994. Summer distribution and habitat use by chinook salmon and steelhead within a major river basin of the South Umpqua River, Oregon. Trans. Am. Fish. Soc. **123**: 298–308.

Rosenfeld, J., Porter, M., and Parkinson, E. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kistuch*). Can. J. Fish. Aquat. Sci. **57**: 766–774.

Swanson, F.J., Benda, L.E., Duncan, S.H., Grant, G.E., Megahan, W.F., Reid, L.M., and Ziemer, R.R. 1987. Mass failures and other processes of sediment production in Pacific Northwest forest landscapes. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. Institute of Forest Resources, University of Washington, Seattle, Wash. pp. 9–38.

Tabachnick, B.G., and Fidell, S. 1996. Using multivariate statistics. HarperCollins, New York.

Titus, K., and Mosher, J.A. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. Am. Midl. Nat. **111**: 1–7.

Trotter, P.C. 1989. Coastal cutthroat trout: a life-history compendium. Trans. Am. Fish. Soc. **118**: 463–473.

Watson, G., and Hillman, T.W. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at heirarchical scales. N. Am. J. Fish. Manag. **17**: 237–252.

Wydoski, R.S., and Whitney, R.R. 1979. Inland fishes of Washington. University of Washington Press, Seattle, Wash.

Ziemer, R.R., and Lisle, T.E. 1998. Hydrology. *In* River ecology and management: lessons from the Pacific coastal ecoregion. *Edited by* R.J. Naiman and R.E. Bilby. Springer-Verlag, New York. pp. 43–68.

© 2003 NRC Canada

PERSPECTIVE / PERSPECTIVE

Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition

Edward D. Weber and Kurt D. Fausch

Abstract: Competition between hatchery-reared and wild salmonids in streams has frequently been described as an important negative ecological interaction, but differences in behavior, physiology, and morphology that potentially affect competitive ability have been studied more than direct tests of competition. We review the differences reported, designs appropriate for testing different hypotheses about competition, and tests of competition reported in the literature. Many studies have provided circumstantial evidence for competition, but the effects of competition were confounded with other variables. Most direct experiments of competition used additive designs that compared treatments in which hatchery fish were introduced into habitats containing wild fish with controls without hatchery fish. These studies are appropriate for quantifying the effects of hatchery fish at specific combinations of fish densities and stream carrying capacity. However, they do not measure the relative competitive ability of hatchery versus wild fish because the competitive ability of hatchery fish is confounded with the increased density that they cause. We are aware of only two published studies that used substitutive experimental designs in which density was held equal among treatments, thereby testing for differences in competitive ability. Additional substitutive experiments will help managers to better understand the ecological risk of stocking hatchery fish.

Résumé : La compétition entre les salmonidés de pisciculture et les salmonidés sauvages est fréquemment décrite comme une importante interaction écologique négative; cependant, on a plus souvent étudié les différences de comportement, de physiologie et de morphologie qui affectent potentiellement la capacité de faire compétition que testé directement la compétition. Nous faisons une revue des différences signalées, des plans d'expérience appropriés aux diverses hypothèses concernant la compétition, ainsi que des tests de compétition décrits dans la littérature. Plusieurs études fournissent des preuves indirectes de la compétition, mais les effets de la compétition ne sont pas séparés de ceux d'autres variables. La plupart des expériences directes sur la compétition ont un plan d'expérience avec additions qui compare des situations où l'on ajoute des poissons de pisciculture à des habitats contenant des poissons sauvages à des situations témoins sans addition de poissons de pisciculture. Ces études sont adéquates pour quantifier les effets des poissons de pisciculture à des combinaisons particulières de densités de poissons et de stocks limites. Cependant, elles ne mesurent pas la capacité relative de compétition des poissons de pisciculture par rapport aux poissons sauvages, car la capacité de compétition des poissons de pisciculture est masquée par l'augmentation de densité qu'ils causent. Seulement deux études publiées, à notre connaissance, ont un plan d'expérience avec substitutions dans lequel les densités sont maintenues constantes dans tous les traitements, si bien qu'elles mettent à l'épreuve les différences de capacité de compétition. De futures études de substitution permettront aux gestionnaires de mieux comprendre les risques écologiques des empoissonnements avec des poissons de pisciculture.

[Traduit par la Rédaction]

Introduction

Hatcheries have played an important role in supporting the harvest and conservation of many salmonid species, and hatchery-reared fish now make up large proportions of some stocks (e.g., Flagg et al. 1995; Unwin and Glova 1997). Nevertheless, hatchery use has become increasingly controversial because of the potential for negative interactions

Received 2 December 2002. Accepted 14 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 30 September 2003.
J17213

Edward D. Weber[1] and Kurt D. Fausch. Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523-1474, U.S.A.

[1]Corresponding author (e-mail: weber@cnr.colostate.edu).

 doi: 10.1139/F03-087 © 2003 NRC Canada

between hatchery-reared (hatchery) and naturally spawned (wild) fish (White et al. 1995; Einum and Fleming 2001). Stocked fish can negatively affect wild fish through genetic contamination, predation, competition, induction of premature migration, mixed-stock exploitation problems, predator attraction, and disease transmission (White et al. 1995). However, the ecological effects of stocking hatchery fish on their wild counterparts have received less attention than genetic effects (e.g., Hindar et al. 1991; Busack and Currens 1995), even though ecological effects may be equally important. Moreover, published studies on ecological interactions have not demonstrated consistent results (Steward and Bjornn 1990; Fresh 1997), in part because many different experimental designs have been used to test hypotheses that differ subtly. Differences in behavior, morphology, and physiology between hatchery and wild fish also likely affect the outcome of ecological interactions such as competition. These differences can be so great that Gross (1998) described Atlantic salmon (*Salmo salar*) reared in wild versus aquaculture environments as "one species with two biologies" and proposed that the two should be classified as separate species.

In this perspective, we focus on competition between hatchery and wild fish, because competition has frequently been cited as an important negative ecological interaction but has seldom been tested rigorously. We first discuss genetic and environmental mechanisms that produce differences in behavior, morphology, and physiology between hatchery and wild fish that can affect competitive ability, and summarize the differences that have been reported in the literature (cf. Steward and Bjornn 1990; White et al. 1995). We then describe weak versus strong evidence for competition between hatchery-reared and wild fish, experimental designs appropriate for asking different questions about intraspecific competition, and tests of competition reported in the literature. We conclude that most studies providing strong evidence for competition were appropriate to quantify the effects of specific hatchery programs on wild fish but not to answer the general question of whether hatchery fish are more or less competitive than wild fish. To clarify terms, we use "wild" to mean fish that are progeny of parents that spawned without human intervention and reared in natural environments, regardless of the origin of the parents, unless stated otherwise. In many cases, stocked fish have successfully spawned under natural conditions, resulting in wild progeny that have been influenced genetically by fish culture.

Differences that potentially affect competitive ability

Hatchery fish differ from their wild counterparts in that their genetic makeup differs to varying degrees depending on the broodstock used by the hatchery and because hatchery-rearing environments are very different than natural streams. Hatcheries typically rear fish at much higher densities than encountered in streams, in lower current velocities, and using different foods and feeding regimes. Consequently, behavioral, morphological, and physiological differences may arise in hatchery-reared fish because of differences in learning, expression of phenotypic traits, and genotypic selection, compared with wild fish reared in natural environments. When interpreting studies that compare hatchery versus wild fish, it is necessary to understand both their genetic background and rearing environment, because different hypotheses can be tested depending on how these factors are controlled. Before summarizing differences between hatchery and wild fish, we describe how hatcheries create phenotypic and genetic differences between the two groups and the different questions that can be tested depending on how genetic and environmental factors are controlled in experiments.

Phenotypic differences between hatchery and wild fish probably result from developmental responses to environment and learning (Fleming et al. 1997; Olla et al. 1998; Einum and Fleming 2001) and from the lower early-life mortality of hatchery fish (Swain et al. 1991; Fleming et al. 1994). Because a larger fraction of the initial cohort survives in the hatchery, differences between wild and hatchery fish may be caused by expression of traits in the hatchery that would be selected against in the wild. That is, wild phenotypes may be a subset of hatchery phenotypes (sensu Miller 1962; Fleming et al. 1994).

Genetic differences between hatchery and wild fish (Hindar et al. 1991; Reisenbichler and Rubin 1999) may be due to local adaptation of stocks or selective mortality caused by the rearing environment. Most characteristics that differ between hatchery and wild salmonids have been reported to have a genetic basis, and many also vary among locally adapted wild populations (Fleming and Gross 1989; Youngson and Verspoor 1998). Because hatchery broodstocks often are not derived from local populations, differences between hatchery and wild fish may be simply due to differences in local adaptations rather than effects of hatchery selection or environment (Chilcote et al. 1986; Reisenbichler and Rubin 1999). However, producing hatchery fish unavoidably causes genetic changes because broodstock fish are chosen artificially rather than by competing for mates in a natural environment in which sexual selection would occur and because some of the greater early-life mortality of wild fish causes selection (Busack and Currens 1995).

Because differences between hatchery and wild fish can be caused by these different mechanisms, comparisons of the two strains test different hypotheses depending on three factors: genetic background, rearing environment, and the environment in which the study was conducted (i.e., testing environment). First, studies that compare hatchery and wild fish of different genetic background but reared in the same environment test for genetically based differences (i.e., a common garden experiment). In this case, the term "hatchery fish" is used to mean the progeny of fish that have been reared in a hatchery for one or more generations, whereas "wild fish" are those that have not been genetically influenced by hatchery releases. Second, studies that compare fish of the same genetic background reared in different environments (e.g., hatchery raceway versus natural stream channel) test for an effect caused by the rearing environment. Here, "hatchery fish" are those reared in the hatchery, and "wild fish" are those reared in the stream. Third, studies that compare fish of different genetic background in different rearing environments test for the combined effects of genetic background and environment. Finally, the testing environment is a nuisance factor in comparing hatchery versus wild fish. Generally, the research question of interest is how the

© 2003 NRC Canada

performance of hatchery and wild fish compare in a natural stream. However, studies often have been conducted in hatcheries, laboratories, or artificial streams to allow for greater experimental control. This testing environment may be important because it probably affects many types of comparisons directly and may also interact with genetic background and rearing environment (Ruzzante 1994; Einum and Fleming 2001). For example, differences between hatchery and wild fish might be expressed to different extents in laboratories versus streams, and the extent to which they are expressed might also depend on genetic background or rearing environment.

For this perspective, we selected the most important studies that tested for differences between hatchery and wild fish in characteristics that potentially affect competitive ability or survival. These include studies using designs that tested for differences resulting from genetic background, rearing environment, or the combined effects of both. Our primary goal is to describe physiological, morphological, and behavioral characteristics that differ between hatchery and wild fish, but we also summarize the genetic and environmental controls used for each study in Table 1. For resident salmonids, our summary includes both juvenile and adult life stages, but for anadromous salmonids, it reflects a bias in the literature toward reporting differences for juveniles. Nevertheless, we report differences for adult anadromous salmonids and other material where appropriate. Unless otherwise stated, we have accepted the authors' conclusions about these differences without evaluating the experimental design or statistical power of each study.

Aggression

Differences in the frequency and intensity of aggressive behavior, such as nips, chases, and lateral or frontal displays, have been commonly reported between hatchery and wild salmonids using several types of experiments. Aggression is directly related to competition because less aggressive fish are often displaced downstream or into energetically less favorable areas of the stream (Mason and Chapman 1965; Fausch 1984). Some studies have compared populations by quantifying the behavior of each group in allopatry (e.g., Moyle 1969; Fenderson and Carpenter 1971; Deverill et al. 1999) or comparing the mean behavior of individual fish matched against themselves in mirrors (Swain and Riddell 1990; Berejikian et al. 1996). Other studies have quantified aggressive behavior of hatchery and wild fish in sympatry (e.g., Fenderson et al. 1968; Bachman 1984) or by using a combination of experiments (e.g., Dickson and MacCrimmon 1982; Berejikian et al. 1996).

Several hypotheses have been proposed to explain why hatchery fish might be more or less aggressive than wild fish. The high densities of fish in hatcheries can suppress the establishment of social dominance structures that commonly occur in streams (Keenleyside and Yamamoto 1962; Jenkins 1971), thereby promoting high aggression after hatchery fish are released. For example, Steward and Bjornn (1990) suggested that hatchery fish appear more aggressive after release into streams because they have not had an opportunity to establish social hierarchies. By comparison, wild fish have already established dominance hierarchies, so aggressive acts to maintain them are needed less frequently. Mesa (1991) also hypothesized that cutthroat trout (*Oncorhynchus clarki*) reared at high density in hatcheries were unable to develop stable social structures and had not learned the trade-off between the benefits of aggressive behavior and its energetic cost. Physiological characteristics of hatchery fish might also influence aggression. Fleming et al. (2002) demonstrated that selection for faster-growing fish by hatcheries (see below) coincides with higher levels of growth hormone, which can increase aggressive behavior in salmonids (Johnsson and Björnsson 1994; Fleming and Einum 1997).

Conversely, Doyle and Talbot (1986) predicted that hatcheries would select for less aggressive fish based on a game-theoretic analysis. Ruzzante's (1994) review of the effects of domestication on aggressiveness concluded that hatcheries could select for either greater or lower aggressiveness depending on the availability and distribution of food in the hatchery. Where food is limited and spatially patchy, aggression may be selected for, and growth depensation can occur as dominant fish monopolize food sources (see Blaxter 1975). However, if food is in excess, aggression may be selected against because more aggressive fish expend energy unnecessarily trying to defend food supplies that are not limiting and, therefore, grow more slowly than disinterested fish. The lack of predators in hatcheries might also select for more aggressive fish (see below).

Most aggression studies reported that hatchery-reared salmonids and their offspring were more aggressive than their wild counterparts. However, these results are not universal (Table 1). Relative aggression in Atlantic salmon may change with fish density (Fenderson and Carpenter 1971), and interactions between density, rearing environment, and testing environment likely occur for other species as well (Ruzzante 1994). Habitat partitioning between hatchery and wild fish of different sizes may also reduce aggression between the two types (Chandler and Bjornn 1988). Relative levels of aggression changed with life stage and size in steelhead (*Oncorhynchus mykiss*; Berejikian et al. 1996). Coho salmon (*Oncorhynchus kisutch*) reared in hatcheries have also been reported to be more aggressive than wild fish as juveniles (Swain and Riddell 1990; Berejikian et al. 1999) but less aggressive than wild fish as returning spawners (Fleming and Gross 1993) or adult broodstock (Berejikian et al. 1997). Fleming et al. (1997) reported that hatchery-reared adult Atlantic salmon returning to spawn in fresh water exhibited similar levels of aggression to their wild counterparts but became involved in more prolonged contests, which resulted in more injuries to hatchery fish. Other studies have reported that hatchery fish use physical forms of aggression such as nips more frequently than do wild fish (e.g., Fenderson et al. 1968; Petrosky and Bjornn 1988; Mesa 1991). Although most studies indicate that hatchery-reared salmonids are more aggressive than their wild counterparts as juveniles, interactions between genetic background, environment, density, life stage, size, and other unknown factors prevent a more detailed conclusion about their relative aggression.

Energy expenditure and feeding

Hatchery-reared salmonids released into streams may be less energetically efficient than wild fish (Table 1), which can

© 2003 NRC Canada

result in lower survival rates for hatchery fish (Mortensen 1977; Bachman 1984). The high-density, scramble-for-food environment of the hatchery probably teaches or selects for behaviors that are inefficient in streams. Several species of hatchery-reared salmonids have been reported to be generally more active (Moyle 1969; McLaren 1979) or to use higher velocity areas of the stream than their wild conspecifics (e.g., Pollard and Bjornn 1973; Petrosky and Bjornn 1988; Mesa 1991). However, in some cases, spatial segregation could have resulted from size differences between wild and hatchery fish (Pollard and Bjornn 1973). Inefficient behavior has also been linked to aggression. For example, excessive aggression reduced time available for feeding by dominant hatchery-reared Atlantic salmon in two laboratory experiments (Fenderson et al. 1968; Fenderson and Carpenter 1971). In an experiment in an artificial stream (Deverill et al. 1999), introduced hatchery brown trout (*Salmo trutta*) continued to expend energy in agonistic encounters with resident wild fish despite failing to displace the wild fish from energetically desirable focal points, and their condition declined as a result. Others have reported hatchery fish winning agonistic encounters with wild fish but then failing to occupy the contested area (Bachman 1984; McMichael et al. 1999).

Potential energy deficits incurred by hatchery fish after release into streams may be compounded by other characteristics such as lower efficiency at feeding on wild prey (reviewed by Olla et al. 1998), reduced stamina or swimming ability (Vincent 1960; Greene 1964; Bams 1967), and higher metabolic rates compared with wild fish (Ersbak and Haase 1983). A small fraction of released hatchery-reared fish may not learn to consume wild prey (Elliott 1975; Maynard et al. 1996; Olla et al. 1998). Other investigators have reported that hatchery fish consume less food (e.g., Sosiak et al. 1979; Ersbak and Haase 1983; Smirnov et al. 1994) or fewer types of prey (Sosiak et al. 1979) than wild fish. Ersbak and Haase (1983) reported that hatchery-reared brook trout (*Salvelinus fontinalis*) consumed similar prey items as wild fish but were slower in switching to new types of prey as seasonal changes altered the relative abundance of invertebrate taxa. Feeding opportunity can also be affected by behavior. Hatchery-reared salmonids have been reported to consume fewer benthic prey than wild salmonids (Sosiak et al. 1979; Maynard et al. 1996) and more terrestrial insects (Johnson et al. 1996) because they tend to occupy positions nearer to the water surface.

Predator avoidance and domestication

Hatchery-reared fish often do not avoid predators as well as wild fish do and, consequently, suffer higher mortality rates (reviewed by Olla et al. 1994, 1998). Mortality can be especially high when predators congregate near large releases of hatchery fish (Beamish et al. 1992; Collis et al. 1995). Acclimation to human disturbance might also selectively increase mortality of hatchery-reared fish because they may exhibit a reduced fright response to humans (i.e., domestication; Vincent 1960; Mead and Woodall 1968; Moyle 1969) and be more vulnerable to angling than wild fish (Marnell 1985). Although ability to avoid predators can be improved with experience (Olla and Davis 1989; Healey and Reinhardt 1995; Olla et al. 1998), hatchery fish may never learn to avoid predators as well as wild fish do (Berejikian 1995), and predator avoidance might be genetically controlled (Johnsson and Abrahams 1991). Lack of experience is generally assumed to be the cause of reduced predator avoidance in hatchery fish (Steward and Bjornn 1990). However, several studies have found differences between offspring of wild and hatchery fish that were reared in a common environment (Table 1). These data suggest that heritable genetic traits related to predator avoidance also exist.

Predator avoidance also might be linked with aggressive behavior of salmonids (Martel and Dill 1993; Fleming and Einum 1997; Olla et al. 1998). In natural settings, there is a trade-off between the energetic gain of foraging and the risk of predation incurred (Grant 1993). However, the lack of predators in hatchery environments may select for fish that aggressively forage for food at the expense of wariness of predators (Johnsson et al. 1996). Furthermore, hatchery fish have high energetic demands because they exhibit higher levels of growth hormone than do wild fish (Fleming and Einum 1997; Fleming et al. 2002) and generally grow more quickly. After release, high levels of growth hormone and concomitant high energetic demands might prompt hatchery fish to forage more under the risk of predation (Johnsson and Björnsson 1994; Johnsson et al. 1996; Fleming and Einum 1997). Although hatchery-reared fish are generally larger than their wild counterparts, potentially reducing their vulnerability to some gape-limited predators, Johnsson and Abrahams (1991) demonstrated that hatchery-reared steelhead foraged under high risk of predation more than did wild fish, despite being equally susceptible to predation by cutthroat trout that were large enough to consume both types of prey.

Hatchery fish have several other traits that potentially affect their susceptibility to predators. The use of positions nearer to the water surface (Vincent 1960; Moyle 1969; Bachman 1984) and with less concealment (Vincent 1960; Ritter and MacCrimmon 1973; Bachman 1984) relative to wild fish probably increases visibility to avian and aquatic predators. Skin coloration patterns related to hatchery rearing (see below) can also increase visibility to predators (Donnelly and Whoriskey 1991).

Dispersal

Fish reared in high-density hatchery conditions may fail to disperse into available habitat when stocked in large numbers (e.g., Symons 1969; also see reviews by Clady (1973) and Cresswell (1981)). Survival and growth of hatchery fish of several species were reported to be inversely related to stocking density (e.g., Mortensen 1977; Egglishaw and Shackley 1980; Hume and Parkinson 1987), presumably because intraspecific competition increases with density in local patches. However, most studies have not compared dispersal of hatchery fish with that of wild fish. Symons (1969) reported that stocked hatchery Atlantic salmon moved less than wild Atlantic salmon in the same stream. Richards and Cernera (1989) reported that hatchery-reared chinook salmon (*Ocorhynchus tshawytscha*) remained near stocking areas but wild salmon also remained concentrated around their natal redds. In general, it seems logical that hatchery fish would disperse less than wild fish given their rearing environment and lack of experience with social structures in streams.

© 2003 NRC Canada

Table 1. Summary of selected studies comparing behavioral and physiological characteristics of wild and hatchery-reared salmonids.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
Aggression					
Fenderson et al. (1968)	Atlantic salmon	Same	Different	Laboratory aquaria	Hatchery fish were more aggressive.
Moyle (1969)	Brook trout	Different	Same	Laboratory aquaria	Hatchery fish were more aggressive but statistically significant in only one of two pairs.
Fenderson and Carpenter (1971)	Atlantic salmon	Same	Different	Laboratory aquaria	Hatchery fish were more aggressive at intermediate or high densities, but wild fish were more aggressive at low densities.
McLaren (1979)	Brown trout	Different	Different	Artificial stream (raceways)	Hatchery fish were more aggressive.
Dickson and MacCrimmon (1982)	Atlantic salmon	Same	Different	Artificial stream	No significant differences in aggression.
Bachman (1984)	Brown trout	Different	Different	Stream	Hatchery fish were more aggressive but did not necessarily benefit from encounters.
Swain and Riddell (1990)	Coho salmon	Different	Same	Laboratory aquaria	Hatchery fish were more aggressive.
Mesa (1991)	Cutthroat trout	Different	Different	Artificial stream	Hatchery fish were more aggressive. Interactions were measured within groups and conducted during different months.
Berejikian et al. (1996)	Steelhead	Different	Same	Laboratory aquaria and artificial stream	Wild swim-up fry were more dominant than hatchery-reared fish. Hatchery fish reared in low-ration flumes were more aggressive than hatchery fish reared in tanks or wild fish reared in either environment.
Peery and Bjornn (1996)	Chinook salmon	Different	Different	Artificial stream	Hatchery fish were more aggressive.
Johnsson et al. (1996)	Brown trout	Different	Same	Laboratory stream tanks	No difference between hatchery and wild fish aggressiveness.
Siikavuopio et al. (1996)	Arctic charr	Same	Different	Laboratory tanks	Wild fish were more aggressive, measured indirectly through fin damage.
Einum and Fleming (1997)	Atlantic salmon	Different	Same	Artificial stream and natural stream	Progeny of farmed fish were more aggressive than wild fish, but hybrids of wild and farmed fish were most dominant.
Fleming and Einum (1997)	Atlantic salmon	Different	Same	Artificial stream and hatchery tank	Hatchery fish were more aggressive in the tank but less aggressive in the artificial stream.
Berejikian et al. (1999)	Coho salmon	Different[a]	Same	Artificial stream	Offspring of hatchery broodstock were more aggressive than identically reared offspring of wild fish.
Deverill et al. (1999)	Brown trout	Different	Different	Artificial stream	Hatchery fish were more aggressive than either resident wild fish or introduced wild fish.
McMichael et al. (1999)	Steelhead	Different	Different	Stream reaches	More physical interactions but fewer threats and displays occurred in sections with hatchery fish than in sections without hatchery fish.
Energy expenditure and feeding					
Fenderson et al. (1968)	Atlantic salmon	Same	Different	Laboratory aquaria	Aggressive interactions among hatchery fish reduced feeding time.

© 2003 NRC Canada

Moyle (1969)	Brook trout	Different	Same	Laboratory aquaria	Hatchery fish swam continuously throughout the water column, whereas wild fish held focal positions near the bottom.
Fenderson and Carpenter (1971)	Atlantic salmon	Same	Different	Laboratory aquaria	Aggressive interactions resulted in a loss of feeding time for hatchery fish at high densities but not at low densities.
Pollard and Bjornn (1973)	Rainbow trout	Different	Different	Stream sections	Hatchery fish occupied deeper, faster water than wild steelhead trout but hatchery fish were larger.
McLaren (1979)	Brown trout	Different	Different	Artificial stream (raceways)	Hatchery fish were more active and aggressive than wild fish.
Dickson and MacCrimmon (1982)	Atlantic salmon	Same	Different	Artificial stream	Hatchery fish occupied mid-water, higher velocity positions in streams, whereas wild fish occupied positions near the bottom.
Bachman (1984)	Brown trout	Different	Different	Stream	Hatchery fish used less profitable positions in the stream, fed less, engaged in more agonistic encounters, and often did not occupy positions won in agonistic encounters.
Petrosky and Bjornn (1988)	Rainbow trout	Different	Different	Stream sections	Hatchery fish used different microhabitat than wild rainbow trout, presumed to be energetically less favorable.
Mesa (1991)	Cutthroat trout	Different	Different	Artificial stream	Hatchery fish used less profitable areas of the stream than wild fish despite similar cover and food availability.
Deverill et al. (1999)	Brown trout	Different	Different	Artificial stream	Introduced hatchery fish were unsuccessful at aggression and used less profitable positions than resident or introduced wild fish, as measured by specific growth rates.
McMichael et al. (1999)	Steelhead	Different	Different	Stream reaches	Hatchery fish did not occupy positions won after agonistic encounters with other fish.
Predator avoidance or domestication					
Vincent (1960)	Brook trout	Different	Same	Laboratory troughs	Hatchery fish used cover less and exhibited a lower fright response to humans than wild fish.
Bams (1967)	Sockeye[b] salmon	Same	Different	Laboratory aquaria	Hatchery fish were more vulnerable to predation by cutthroat trout.
Mead and Woodall (1968)	Sockeye salmon	Same	Different	Laboratory tanks	Hatchery-reared fish avoided light less than fish reared in natural or artificial channels. Predation was greatest on hatchery-reared fish but differences were not statistically significant.
Moyle (1969)	Brook trout	Different	Same	Laboratory aquaria	Hatchery fish exhibited lower fright response to human disturbance than wild fish.
Ritter and MacCrimmon (1973)	Rainbow trout	Same	Different	Laboratory tank	Pond-reared fish used dark substrate. Laboratory reared fish were randomly distributed between light and dark.
Johnsson and Abrahams (1991)	Steelhead	Different	Same	Artificial stream	Hatchery–wild hybrids were more willing to forage under threat of predation than wild fish.
Berejikian (1995)	Steelhead	Different	Same	Artificial stream and seminatural stream	Hatchery fry were preyed on more than wild fry by sculpin.
Johnsson et al. (1996)	Brown trout	Different	Same	Artificial stream	Hatchery–wild hybrids were more willing to forage under threat of predation than wild fish.

© 2003 NRC Canada

Table 1 (*concluded*).

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
Einum and Fleming (1997)	Atlantic salmon	Different	Same	Artificial stream and natural stream	Progeny of farmed fish reappeared from cover sooner after a simulated predator attack than wild fish did. Hybrids of farmed and wild fish were intermediate.
Fleming and Einum (1997)	Atlantic salmon	Different	Same	Artificial stream and hatchery tank	Hatchery fish reappeared from cover sooner after a simulated predator attack than wild fish did.
Johnsson et al. (2001)	Atlantic salmon	Different	Same	Laboratory	Hatchery fish exhibited reduced flight and physiological responses to a simulated predator attack at age 1. At age 2, hatchery and wild fish exhibited similar responses.
Dispersal					
Symons (1969)	Atlantic salmon	?[c]	Different	Stream	Marked wild fish dispersed more than hatchery fish released in the same area, perhaps resulting from competitive interactions between the two groups.
Richards and Cernera (1989)	Chinook salmon	Same	Different	Stream	Hatchery-reared fish remained near stocking sites. Wild fish remained near redds.
Fleming et al. (2000)	Atlantic salmon	Different	Same	Stream	Progeny of farm-reared fish remained closer to redds than wild fish. Hybrids of farm-reared and wild fish moved intermediate distances. Wild fish may have been displaced.
Size and growth					
Vincent (1960)	Brook trout	Different	Same	Hatchery	Progeny of fish domesticated for several generations grew fastest, fish domesticated for one generation were intermediate, and wild fish grew slowest.
Reisenbichler and McIntyre (1977)	Steelhead	Different	Same	Streams and hatchery pond	In a pond, progeny of hatchery fish grew faster than progeny of wild fish or hybrids. In streams, either hybrids grew fastest or there was no significant difference among groups.
Piggins and Mills (1985)	Atlantic salmon	Different	Different	Streams and ocean	Hatchery fish grew faster than wild fish.
Kallio-Nyberg and Koljonen (1997)	Atlantic salmon	Different	Same	Ocean and hatchery	Progeny of farm raised salmon grew faster and matured earlier than progeny of wild salmon.
McGinnity et al. (1997)	Atlantic salmon	Different	Same	Natural stream	Progeny of farm raised salmon grew fastest, hybrids were intermediate or not different from wild fish, and wild fish grew slowest.
Fleming and Einum (1997)	Atlantic salmon	Different	Same	Artificial stream and hatchery tank	Hatchery fish grew faster than wild fish.
Berejikian et al. (1999)	Coho salmon	Different[d]	Same	Artificial stream	There was no difference in growth rates between paternal half-siblings with wild versus hatchery mothers.
Rhodes and Quinn (1999)	Coho salmon	Same	Different	Streams	Fish reared in the hatchery for several months were larger than fish reared in streams and continued to grow faster, when adjusted for size, after being added to streams.
Fleming et al. (2002)	Atlantic salmon	Same	Different	Laboratory	Hatchery fish grew faster than wild fish and exhibited higher levels of growth hormone.

© 2003 NRC Canada

Color					
Berejikian et al. (1999)	Coho salmon	Different[a]	Same	Laboratory	Paternal half-siblings with hatchery mothers were lighter colored than those with wild mothers, which may have provided hatchery fish with a competitive advantage.
Other morphological characteristics and physiological performance					
Philips (1957)	Brook trout	Different	Different	NA	Wild trout bodies contained more protein and ash and less fat and water than hatchery fish.
Bams (1967)	Sockeye salmon	Same	Different	Artificial stream	Fish reared in hatcheries were poorer swimmers than fish reared in streams. Fish moved from hatchery to gravel at an earlier life stage were intermediate.
Hjort and Schreck (1982)	Coho salmon	Different	Different	NA	Morphology of juvenile hatchery-reared salmon from several hatcheries were more similar to each other than to any of several wild populations examined.
Piggins and Mills (1985)	Atlantic salmon	Different	Different	Streams and ocean	Some hatchery fish exhibited vertebral compaction not generally seen in wild fish.
Taylor (1986)	Coho salmon	Different[d]	Different	NA	Body shapes of juvenile hatchery-reared salmon from several hatcheries were more similar to each other than to nearby wild populations, which varied regionally.
Woodward and Strange (1987)	Rainbow trout	Different	Different	Laboratory	Hatchery fish exhibited a lower plasma cortisol and plasma glucose response to stress than wild fish.
Fleming and Gross (1989)	Coho salmon	Different	Different	NA[e]	Body shape of wild adult females varied across populations with intensity of breeding competition. Body shape of adult females of hatchery origin had characteristics consistent with least breeding competition.
Swain et al. (1991)	Coho salmon	Both	Both	NA	Body shapes differed between hatchery and wild fish. Environmental effect was larger than genetic effect.
Fleming et al. (1994)	Atlantic salmon	Both	Different	NA	First generation farm-reared salmon had different body shape than genetically similar wild fish. Differences were heritable and increased with successive farmed generations. Fleming and Einum (1997)

[a]Hatchery and wild fish were paternal half-siblings.
[b]*Oncorhynchus nerka*.
[c]Hatchery fish were from "wild parents".
[d]Most hatchery fish were from "wild stock".
[e]Not applicable.

© 2003 NRC Canada

However, it has yet to be demonstrated that dispersal behavior is different between wild and hatchery fish when the two groups are not influencing each other.

Size and growth

Hatchery fish are usually larger and faster growing than their wild counterparts of the same cohort, in part because hatcheries often select broodstock that mature and spawn early (Vincent 1960; Reisenbichler and McIntyre 1977; Fleming et al. 2002) and in part because the hatchery diet and environment results in faster-growing fish (Piggins and Mills 1985; Rhodes and Quinn 1998; Berejikian et al. 1999). It is difficult to determine the causes of accelerated growth in the hatchery because genetic effects are confounded with the hatchery diet, water temperature, and other environmental factors (Blaxter 1975; Einum and Fleming 1999). However, hatchery-reared fish or their progeny sometimes grow faster after release into natural streams than wild fish of the same or smaller initial sizes (e.g., Petersson et al. 1996; McGinnity et al. 1997; Kallio-Nyberg and Koljonen 1997). These data suggest that accelerated growth of hatchery fish is not only due to rearing conditions in the hatchery, but also to genetic differences or persistent phenotypic effects.

The larger size and faster growth of hatchery fish probably also reflects differences in selective pressure between hatchery and natural environments. Hatchery rearing may cause selection for early emergence and fast growth because fish that emerge early and grow quickly generally have a competitive advantage over smaller fish (Mason and Chapman 1965; Metcalfe and Thorpe 1992). Furthermore, size at first winter or smolting has been directly linked with survival rate for a number of salmonid species (see Quinn and Peterson (1996) for a review). There are few disadvantages to early emergence in the hatchery; so early emergence is probably reinforced by natural selection. However, other factors may select against early emergence in natural streams. Early emergence relative to conspecifics can result in higher susceptibility to predation (Braunnas 1995), catastrophic floods (e.g., Seegrist and Gard 1972; Fausch et al. 2001), or a mismatch with ocean productivity (Hartman et al. 1982; Holtby 1988).

As a consequence of their larger size, juvenile hatchery fish may be able to outcompete smaller wild fish (Nickelson et al. 1986; Rhodes and Quinn 1998; Berejikian et al. 1999). However, in some cases, wild anadromous salmonids may increase their growth rates by emigrating to sea before hatchery fish are released, thereby reaching similar sizes by the time hatchery fish reach the ocean and potentially compete with them (Unwin and Lucas 1993).

Color

Hatchery-reared salmonids are generally lighter in color than salmonids reared in natural environments because hatchery-reared fish adjust to the background color of the raceways in their rearing environment (Donnelly and Whoriskey 1991; Maynard et al. 1995). Hatchery fish can change their general coloration within minutes using chromatophores. However, developing the pigments and chromatophore patterns to match the background of a new stream environment can take weeks (Maynard et al. 1995). Berejikian et al. (1999) suggested that the diet of captive broodstock could also reduce pigmentation in eggs and subsequently alter fry coloration.

In addition to affecting susceptibility to predators, differences in coloration between wild and hatchery-reared fish may influence the outcome of competitive interactions. Dominant salmonids generally remain lighter colored, whereas subordinate fish assume darker body coloration to signal submission (e.g., Rosenau and McPhail 1987; Berejikian et al. 1999), although contrast between coloration of the body and parr marks or fins might be a more important signal of dominance or submission (cf. Keenleyside and Yamamoto 1962; Fenderson et al. 1968; Taylor and Larkin 1986). Differences in coloration that allow fish to signal their status may reduce the need for aggressive interactions (Berejikian et al. 1999), but hatchery-reared salmonids may be less able to assume submissive coloration patterns than wild fish. The inability to signal submission could prolong aggressive encounters between wild and hatchery fish or allow hatchery-reared fish to assume dominant positions in streams as competing wild fish become exhausted (Berejikian et al. 1999). The effect of color on hatchery versus wild fish interactions is generally confounded with other characteristics that differ between the two groups such as size, rearing environment, and innate aggression. Furthermore, salmonid markings may be local adaptations (Taylor and Larkin 1986), possibly confounding comparisons between wild fish and hatchery-reared fish from different genetic backgrounds. These difficulties have, thus far, prevented any conclusive determination of the effects of color on competition between hatchery-reared and wild fish.

Other morphological characteristics and physiological performance

Several other morphological and physiological performance characteristics differ between wild and hatchery-reared salmonids and potentially affect competitive ability. After several generations of domestication, the body composition of hatchery fish is generally made up of more fat and less protein than that of wild fish (Phillips 1957; Vincent 1960; Blaxter 1975). Hatchery selection and environment may alter internal and external morphology (e.g., Hjort and Schreck 1982; Taylor 1986; Gross 1998), which can influence swimming, spawning success, and survival (Taylor 1986; Gross 1998). Hatchery-reared fish have been reported to be poorer sustained swimmers than wild fish (Vincent 1960; Greene 1964; Bams 1967) and to exhibit a reduced fight-or-flight response to stress (Woodward and Strange 1987; Salonius and Iwama 1993; Johnsson et al. 2001). Anadromous salmonids reared in hatcheries may be physiologically less prepared to smolt than wild fish (Brauner et al. 1994; Shrimpton et al. 1994). Several studies have demonstrated that morphological characteristics of hatchery-reared fish are more homogeneous across a large geographical range than are wild fish in the same range (Hjort and Schreck 1982; Taylor 1986; Fleming and Gross 1989). These data suggest that rearing practices promote characteristics that are better adapted to hatcheries, which are similar throughout much of the world, than to local conditions that affect survival in the wild.

Prior residence

Competitive interactions between wild and hatchery fish can be influenced by the fact that wild fish typically reside in streams before hatchery fish are stocked. Because prior residence is not a physiological, morphological, or behav-

© 2003 NRC Canada

ioral characteristic of fish, we describe the evidence for an effect of prior residence on competition but do not summarize studies of prior residence in Table 1. The advantage of prior residence in territory defense has been documented for both intraspecific (e.g., Chapman 1962; Rhodes and Quinn 1998; Gowan and Fausch 2002) and interspecific interactions among salmonids (e.g., Glova and Field-Dodgson 1995). Acclimation for as little as one day can confer an advantage to the residents in social interactions over newly introduced fish (Huntingford and Garcia De Leaniz 1997). Fish are assumed to learn the benefits conferred by residing in an area and the relative cost of defending it (Grant 1993; Johnsson et al. 1999).

The advantage of prior residence can be overcome by body size (Rhodes and Quinn 1998; Gowan and Fausch 2002), but the two are related in natural systems. Fish that emerge earlier are the first to establish territories and normally gain a size advantage, sometimes prompting fish that emerge later to emigrate (Mason and Chapman 1965; Chandler and Bjornn 1988; Metcalfe and Thorpe 1992). Deverill et al. (1999) reported that adult and subadult prior-resident brown trout held a growth advantage over other introduced wild brown trout and an even greater advantage over introduced hatchery brown trout. However, they believed that the larger advantage over hatchery fish was due to unnecessary expenditure of energy by hatchery fish. As with most comparisons above, fish density, environment, and distribution of food may interact to alter the relative advantage of prior residence (Huntingford and Garcia De Leaniz 1997).

Most studies that have identified a strong prior-residence effect have used size-matched fish (e.g., Cutts et al. 1999; Deverill et al. 1999). The advantage that prior residence affords wild fish may be negated by larger or faster-growing hatchery fish (Glova and Field-Dodgson 1995; Rhodes and Quinn 1998). On the other hand, prior residence may confer benefits independent of physical dominance over territories. O'Connor et al. (2000) demonstrated that juvenile Atlantic salmon with prior residence could gain a feeding advantage by darting nearer to the water surface to get food items without excluding or dominating immigrants. In this case, wild fish with prior residence used their knowledge of the territory to achieve greater net energy gain, despite sometimes becoming subordinate to larger hatchery fish.

Evidence for competition

Competition occurs when multiple organisms exploit a common resource and the fitness of at least one is reduced, because either the resource is in short supply or other organisms interfere with its use (Birch 1957). Competition may be demonstrated by showing a reduction in one or more measures of fitness, such as growth, fecundity, or survival, when organisms are in sympatry compared with allopatry. To provide strong evidence of competition, it is necessary to conduct replicated, controlled, manipulative experiments (Underwood 1986; Fausch 1988, 1998). Furthermore, it is desirable for experiments to mimic the natural environment as closely as possible so that the relevant hypothesis is tested; that is, do the experimental organisms compete in the wild (Underwood 1986; Fausch 1988)?

Because conducting controlled experiments in natural settings is difficult, much of the evidence for competition between wild and hatchery-reared salmonids is based on less direct or rigorous studies. For example, many researchers concluded that competition is occurring between hatchery and wild fish because one group had lower survival than the other when they were in sympatry. Attributing differences in survival rates to competition is tenuous for uncontrolled studies, particularly given the innate differences between the two groups described above that probably cause survival rates to differ (cf. Wales 1954). However, many studies designed to answer other research questions have provided circumstantial evidence for competition. Therefore, we first summarize the weak evidence for competition before describing studies that tested for displacement of wild fish by hatchery fish or directly tested for competition.

Weak evidence for competition

Many researchers have hypothesized that survival of hatchery fish was reduced by competition with wild fish based on early research designed to evaluate only hatchery fish survival or availability to anglers (e.g., Schuck 1948; Flick and Webster 1964). These studies measured hatchery fish survival and sometimes growth, but only in sympatry with wild fish (i.e., no controls), and often no comparable estimates were made for wild fish. These studies were appropriate to determine the contribution of stocked fish to the fishery, but not to determine the relative importance of competition, behavior, or other mechanisms affecting survival of hatchery or wild fish. Hatchery fish survival relative to wild fish was reported to be lower (Schuck 1948; Vincent 1960; Flick and Webster 1964), similar (Adelman and Bingham 1955), or dependent on season (Mason et al. 1967). In general, too many confounding variables were present in these studies to draw clear conclusions about competitive interactions between wild and hatchery fish.

More recent studies that have held wild and hatchery fish in sympatry to examine other interactions between the two provide limited evidence for competition, but results have also been inconsistent. Survival of hatchery-reared fish has been reported to be higher (Berejikian et al. 1999; Reinhardt et al. 2001), lower (Leider et al. 1990; Berg and Jorgensen 1991; Einum and Fleming 2001), or equal (Rhodes and Quinn 1999) to that of wild fish. Competition likely played a role in at least some of the results. Berejikian et al. (1999) suggested that competition with fry from hatchery stock influenced survival of wild coho salmon in an experimental flume because more wild fish died of apparent starvation at the downstream end of the flume than at the upstream end, where food was not limiting. McGinnity et al. (1997) and Fleming et al. (2000) reported that Atlantic salmon with hatchery genetic backgrounds exhibited higher early-life mortality than did Atlantic salmon with wild genetic backgrounds when both types were reared similarly before release, but surviving hatchery fish outgrew and probably displaced their wild counterparts.

Correlational studies that documented population increases or establishment of hatchery fish when wild fish declined, or vice versa, also provide limited support for the hypothesis that competition is occurring. Seelbach (1987) and Seelbach and Whelan (1988) speculated that higher sur-

© 2003 NRC Canada

vival and adult returns of hatchery steelhead in Great Lakes streams with low densities of naturally reproducing steelhead was due to reduced competition. Campton and Johnston (1985) suggested that successful establishment of hatchery-reared rainbow trout in the upper Yakima River, Washington, was due to reduced competition, because populations of native steelhead had declined. Likewise, Volpe et al. (2001) hypothesized that Atlantic salmon escaping from farms may be colonizing the North Pacific Ocean, despite many failed introduction attempts during the early 20th century, because native salmonid populations have declined.

Similar studies have reported decreases in wild populations concurrent with stocking, or increases in wild populations when stocking ceased. Bjornn (1978) reported that wild populations of rainbow trout declined when steelhead fry were stocked in the Lemhi River, Idaho. Vincent (1987) reported that densities of wild rainbow trout and brown trout increased after stocking of adult hatchery rainbow trout ceased in two Montana streams. However, concurrent changes in river discharge were confounding. Furthermore, hatchery fish were smaller than the resident wild fish in this case, making it less likely that the wild fish were outcompeted (cf. Petrosky and Bjornn 1988). Thuemler (1975) has frequently been cited as evidence of competition among wild and hatchery-reared trout in streams. He stated that wild trout populations increased in several Wisconsin streams after stocking ceased, apparently based on correlational studies, but the article does not report any specific data.

Other studies reported that hatchery-reared anadromous fish have replaced wild fish in the ocean (e.g., Pearcy 1997; Unwin and Glova 1997; Hilborn and Eggers 2000). Competition from hatchery fish may play a role in reducing ocean survival of wild fish, but mixed-stock exploitation problems (McIntyre and Reisenbichler 1986; Hilborn and Eggers 2000; Noakes et al. 2000) and genetic dilution (Flagg et al. 1995; Unwin and Glova 1997) probably also are important factors. Although studies of ocean interactions are limited because estimates of wild fish survival are unavailable (Winton and Hilborn 1994), the hypothesis of competition is supported by recent studies that indicate a stronger negative effect of hatchery fish when ocean conditions are less favorable for salmonids so that carrying capacity is presumably reduced (Pearcy 1997; Beamish et al. 1997; Levin et al. 2001).

Overall, the weak evidence for competition demonstrates that survival rates often differ between hatchery and wild fish in sympatry and suggests that competition differentially influences survival rates in some cases. However, competition cannot be demonstrated strictly by these studies because the effects of competition are confounded with physiological, morphological, and behavioral differences between hatchery and wild fish that also affect survival.

Displacement

A more direct type of evidence for competition is the displacement of wild fish from territories or focal positions by hatchery fish. Although competition has not strictly been demonstrated unless survival, growth, or reproduction of displaced fish has been reduced, these studies provide information about the relative ability of hatchery versus wild fish to compete for space. Stream salmonids compete for positions that are energetically favorable in terms of food availability and refuge from current (Metcalfe 1986; Hughes 1992), and fish that occupy more favorable positions grow faster (Fausch 1984). Studies that measure solely displacement rely on the logical inference that when stream positions are limited, displaced fish are forced into less favorable areas and consequently suffer reduced fitness.

Displacement of wild fish by hatchery fish has been reported in both small-scale laboratory experiments and natural streams. Fenderson et al. (1968) found that hatchery-reared juvenile Atlantic salmon attained dominant positions in aquaria over wild fish. However, a subsequent experiment revealed that wild fish dominated when overall densities were lowered to levels similar to those in streams (Fenderson and Carpenter 1971). Einum and Fleming (1997) reported that farmed Atlantic salmon dominated wild fish in one-on-one challenges, with hybrids exhibiting intermediate success. Similarly, in one-on-one challenges in aquaria, juvenile hatchery-reared coho salmon overcame both size-matched stream-reared fish from the same parental stock and smaller wild fish (Rhodes and Quinn 1998). Berejikian et al. (1999) reported that juvenile coho salmon with mothers from hatchery broodstock won dominance challenges in a laboratory flume more frequently than paternal half-siblings with wild mothers, thereby demonstrating a maternal effect. On the other hand, Peery and Bjornn (1996) reported no consistent effect of adding hatchery juvenile chinook salmon on wild chinook salmon emigration from laboratory flumes.

Displacement of wild fish by hatchery fish has also been directly observed in streams among steelhead or rainbow trout (Pollard and Bjornn 1973; McMichael et al. 1999, 2000), coho salmon (Nielsen 1994), and chinook salmon, but only when the hatchery chinook salmon were larger (Peery and Bjornn 1996). In contrast, Bachman (1984) reported that nearly equal proportions of hatchery and wild adult brown trout dominated agonistic encounters, but wild trout that were dominant before hatchery fish were added rarely were displaced. Hatchery fish are typically larger than wild fish, which may decrease encounters that result in displacement (Pollard and Bjornn 1973; Petrosky and Bjornn 1988; Nielsen 1994). For example, Petrosky and Bjornn (1988) reported that stocked rainbow trout rarely displaced wild rainbow trout because the hatchery fish were larger and occupied deeper water.

Displacement of wild fish may also occur at the reach scale after hatchery fish are stocked. Symons (1969) and McGinnity et al. (1997) reported that wild fish emigration rates from stream sections enclosed by weirs increased after hatchery fish were stocked. Fleming et al. (2000) reported that wild Atlantic salmon fry were displaced upstream as progeny of farm-reared Atlantic salmon developed into fry. Alternatively, increased emigration rates may be due to wild fish schooling with newly released hatchery fish that are also emigrating, termed the "pied-piper effect" (Hansen and Jonsson 1985; Hillman and Mullan 1989). Overall, studies of displacement generally indicate that hatchery fish have equal or greater ability to seize profitable feeding positions, at least as juveniles, which should increase their fitness over wild fish that are relegated to less favorable positions.

© 2003 NRC Canada

Displacement can also be a direct measure of competition when adults compete for spawning areas or mates. Hatchery-reared anadromous salmonids that return to natural streams to spawn have been reported to be less competitive for mates than wild fish (e.g., Fleming and Gross 1993; Berejikian et al. 1997; Fleming et al. 1997) and, consequently, to contribute less to subsequent population production (reviewed by Fleming and Petersson (2001)). However, testing this type of competition may require specialized experimental designs because hatchery fish are both competitors and mates with wild fish. Therefore, we do not address competition for mates further here.

Table 2. Experimental designs to test the existence and strength of intraspecific competition between wild and hatchery-reared fish (adapted from Fausch 1998).

	Treatment				
	1	2	3	4	5
Wild fish	2W	W	W		
Hatchery fish			H	H	2H
			Additive designs • effect of competition		
			Substitutive designs • strength of competition		

Note: W, number of wild fish; H, number of hatchery fish. Treatments 1–3 measure effects of competition on wild fish. The comparison of wild fish in treatment 2 versus treatment 3, an additive design, measures the effect of adding hatchery fish on wild fish. The comparison of treatment 1 versus treatment 3, a substitutive design, measures the relative competitive ability of hatchery versus wild fish, controlling for density. Treatments 3–5 may be used similarly to test the effects of wild fish on hatchery fish relative to areas with no wild fish. See text for more detail.

Strong evidence for competition

Controlled experiments are required to provide strong evidence for competition between hatchery and wild fish. Appropriate designs for such experiments are analogous to the two designs for testing interspecific competition (Underwood 1986; Fausch 1988, 1998; Table 2), but the questions are different when testing for intraspecific competition between hatchery and wild fish. From the standpoint of wild fish conservation, there are two relevant questions about competition with hatchery fish. First, to what extent do hatchery fish compete with wild fish when viewed as a perturbation or invader? Additive experiments are designed to answer this question. Second, is the effect of adding hatchery fish different from the effect of adding wild fish to reach the same total density? For example, if wild fish populations recovered and increased to the point where stocking were no longer necessary, would density-dependent effects among wild fish be equal to the effects of adding hatchery fish, indicating that hatchery and wild fish are competitively equivalent? Substitutive experiments are designed to answer this question.

Additive experiments, designed to quantify the effects of stocking hatchery fish on wild fish, are those in which the number of wild fish is held constant between treatment and control groups but hatchery fish are added to the treatment group (i.e., comparisons of wild fish in treatments 2 and 3 in Table 2). This design incorporates the features of classic experimentation because it holds all things equal between treatments except the perturbation of stocking hatchery fish. However, the interpretation of intraspecific experiments in which hatchery fish are added is slightly different than competition experiments in which another species is added. Interspecific competition experiments are used to test the existence of competition, that is, whether there is any niche overlap between the two species. In contrast, the magnitude of effects is of more interest than their existence in intraspecific competition experiments in which hatchery fish are added. This is because resource use almost certainly overlaps between hatchery and wild fish of the same species despite the differences in behavior and morphology described above, so competition is expected at some density. As a result, effects of hatchery fish will likely be a function of the density of each group, the carrying capacity of the testing environment, and the relative competitive ability of hatchery versus wild fish.

An important feature of additive experiments is that any effect of increased competitive ability of hatchery fish over wild fish cannot be separated from effects of the increased density they cause (cf. Fausch 1998). As a result, this design is useful only to estimate effects of hatchery fish at specific combinations of wild and hatchery fish density and stream carrying capacity and cannot be generalized to other combinations or streams. For example, if hatchery fish were stocked at a given density into a stream with wild fish, the degree to which hatchery fish affect wild fish survival and growth would change if stocking density or wild fish density changed, and the effects would be different in a stream with a different carrying capacity, even if all else were equal. Therefore, additive designs are most appropriate to measure the effects of specific stocking programs in which hatchery fish are introduced at the same density in streams with similar wild fish densities and carrying capacities.

In contrast, substitutive designs measure the relative competitive ability of wild versus hatchery fish. In this design, the density of wild fish in the control group equals the total density of fish (hatchery plus wild) in the treatment group (i.e., comparison of treatments 1 and 3 in Table 2). Substitutive experiments determine whether the effect on wild fish of adding hatchery fish is any different than increasing the density of wild fish by the same amount. For example, if the growth of wild fish is reduced when hatchery fish are added more than when an equal density of wild fish are added, one can infer that hatchery fish are more competitive than wild fish. Although the degree to which hatchery fish affect wild fish will depend on the densities of fish used and the carrying capacity of the testing environment, in substitutive experiments, this effect size is of less interest than whether adding hatchery fish has any greater effect than adding wild fish and whether this effect is biologically significant. That is, the question of whether stocking hatchery fish has a greater ecological cost to wild populations than if wild fish were added is probably of greater interest than the

© 2003 NRC Canada

question of how near to carrying capacity was the testing environment in which the experiment was conducted. Therefore, substitutive designs are most appropriate to determine whether competitive differences between particular races of hatchery fish and wild fish exist.

From the perspective of hatchery fish success, similar additive and substitutive designs can be used to evaluate the magnitude of competition with wild fish and the relative competitive ability of hatchery fish. For example, additive designs that compare controls with hatchery fish alone to treatments with hatchery plus wild fish (treatments 3 and 4; Table 2) measure the relative benefit to hatchery programs of stocking unoccupied streams versus streams with wild populations. However, substitutive designs that compare treatments with wild plus hatchery fish with those with an equal total density of hatchery fish (treatments 3 and 5; Table 2) are of less interest. This experiment tests whether the effect on hatchery fish of adding wild fish is any different than increasing the density of hatchery fish by the same amount. However, we are not aware of any management program in which wild fish are intentionally removed and replaced with hatchery fish. We note that substitutive experiments have a one-way interpretation because the effect of competition is controlled only for the group that is replaced. For example, hatchery fish could have the same effect on wild fish as an equal increase in wild fish density (treatments 1 and 3; Table 2), but the hatchery fish could still lose fitness through inefficient behaviors (McGinnity et al. 1997; Einum and Fleming 2001; Bohlin et al. 2002). Finally, the number of hatchery and wild fish used need not be equal in any of the experimental designs above, provided that the interpretation is one-way (cf. Underwood 1986). Instead, the numbers used should reflect densities of wild fish in natural habitats and the densities of hatchery fish that are stocked.

In the previous discussion, we assumed that the numbers of fish were changed to manipulate density, but the size of experimental units and carrying capacity were held constant. It is also possible to manipulate density by keeping numbers of fish constant across experimental units but changing the area of the units. Such designs could also be used to test whether competitive ability changes with density (e.g., Fleming and Gross 1993, 1994). For example, juvenile hatchery fish might be more competitive than wild fish at high densities that are similar to the hatchery environment but less competitive at lower densities (Fenderson and Carpenter 1971). However, given the high variation that has generally been reported in studies of competition even at single-density combinations (e.g., Peery and Bjornn 1996; McMichael et al. 1997), it is often logistically impossible to conduct experiments at multiple densities with great enough replication to simultaneously test the effects of density, competition, and their interactions.

Studies using an additive design

Most studies reported in the literature have used additive designs to examine the effects of hatchery fish on wild fish. For example, Petrosky and Bjornn (1988) studied the effects of stocking adult hatchery rainbow trout at several densities on wild rainbow trout and cutthroat trout growth, movement, and survival. Wild fish mortality increased only at the highest stocking density. However, total mortality of wild fish subject to hatchery fish stocking did not differ significantly from control groups later in the year, because of either compensation in the survival rate of remaining wild fish or small-sample error. No significant effects were measured for wild fish at lower stocking densities of hatchery fish. A study of Oregon streams (Nickelson et al. 1986) revealed that density of wild coho salmon juveniles was lower in 15 streams stocked with hatchery coho salmon than in 15 similar unstocked streams. The final density was only slightly higher in stocked streams, suggesting that hatchery coho salmon had largely replaced wild fish. The original stocking probably caused the streams to be well above carrying capacity in this study (Flagg et al. 1995). Nielsen (1994) reported reduced production of wild coho salmon after hatchery coho salmon were stocked in the Noyo River, California. Production was also lower than in similar unstocked streams, although not significantly so. Weiss and Schmutz (1999) reported that wild brown trout growth was reduced in sections of a crystalline stream in Austria in which densities were doubled or tripled by stocking hatchery brown trout, but unaffected in a limestone stream that was probably more productive. However, wild trout abundance did not change significantly in either stream. McMichael et al. (1997, 2000) reported that wild rainbow trout growth was lower in 1-m^2 enclosures containing one wild trout and one hatchery-reared steelhead than in enclosures containing one wild trout only. In general, these studies indicated that survival or growth of wild fish was reduced when densities were increased to high levels by stocking hatchery fish. The studies confirm that competition from hatchery fish can reduce fitness of wild fish, but the magnitude of the effect depends on densities of both groups and environmental conditions.

A few studies have used additive designs to study the effects of wild fish on the success of hatchery fish (i.e., treatments 3 and 4; Table 2). Miller (1955, 1958, 1962) conducted a series of experiments using adult cutthroat trout in stream sections. Survival of hatchery fish was much lower in sections that contained wild fish than in sections with hatchery fish only. The density of wild fish was not reported, but Miller (1962) found few wild fish deaths, suggesting that wild fish outcompeted the hatchery fish. Needham and Slater (1944) reported that survival and growth of hatchery brown trout and rainbow trout was inversely related to the biomass of wild trout present in experimental stream sections, but wild fish growth and mortality were not known in this study either. These studies indicate that competition from wild fish can reduce fitness of hatchery fish in certain circumstances but the effect is density-dependent, as above.

Studies using a substitutive design

We are aware of only two experiments that used a substitutive design suitable for testing the strength of competition from hatchery fish relative to wild fish. Peery and Bjornn (1996) used treatments 1, 3, and 5 in Table 2 to examine competition among hatchery and wild chinook salmon in laboratory channels. Although they found that hatchery fish were more aggressive than wild fish and able to displace wild fish from favorable stream positions when the hatchery fish were larger, they did not find consistent effects on

© 2003 NRC Canada

growth, mortality, or emigration. The study was well designed, but it was limited by a scarcity of wild fish and had low statistical power. Furthermore, replicates were conducted during different periods throughout the year because wild fish could not be caught in sufficient numbers to conduct all replicates at the same time. Consequently, the wild fish were larger than the hatchery fish during three seasons, a situation that rarely occurs in streams that are stocked.

Bohlin et al. (2002) used a substitutive design to test the effects of hatchery brown trout on wild brown trout in Swedish streams. The effect on wild fish growth and survival of adding hatchery fish did not significantly differ from the effect of adding wild fish. However, hatchery fish lost condition, presumably because they were inefficient at swimming or foraging, even though they apparently exploited resources to the same degree as wild fish.

Competition experiments can be used to test specific hypotheses about genetic or environmental effects on relative competitive ability, just as comparisons of morphological or behavioral characteristics can. All of the additive studies cited above reared hatchery and wild fish in their home environments and did not specifically control for genetic background, thereby testing for combined effects of hatchery genetic selection and rearing environment. Both substitutive studies used hatchery fish that were genetically similar to the wild fish with which they competed. Peery and Bjornn (1996) used hatchery fish from a supplementation program that attempted to avoid artificial selection and retain genetic frequencies similar to those of wild fish. Bohlin et al. (2002) used hatchery-reared fish that were the progeny of locally obtained wild fish. Further research that holds genetic background or rearing environment constant could be used to determine the relative importance of genetics and environment on competitive ability. Such designs would be particularly useful in conjunction with substitutive experiments to allow general conclusions to be drawn for other streams.

Conclusions

Despite the growing concern about the effects of stocking hatchery fish on wild fish, relatively few experiments of competition between hatchery and wild salmonids have been published. The large body of literature demonstrating differences between hatchery and wild fish suggests that competitive differences may exist between the two groups. However, the ecological consequences of these differences, including competition in natural streams, have not been quantified in most cases.

Nearly all studies of competition between hatchery and wild stream salmonids have used additive experimental designs. These designs are appropriate to answer management questions regarding the impact of stocking hatchery fish at specific densities and stream carrying capacities, if the testing environment is similar to natural conditions and the densities closely match the stocking program of interest. If the experiment is not conducted using the hatchery fish and rearing environment of interest, in streams like those of interest, and using densities that match the stocking program, then the results are likely to be irrelevant to the management question. Additive experiments also frequently have been misinterpreted as evidence that hatchery fish are more or less competitive than wild fish, but substitutive designs are necessary to test this hypothesis.

Almost no studies that used substitutive experimental designs suitable for testing relative competitive ability have been conducted. Additional research using this design should be of broad interest because it would quantify the ecological cost of stocking hatchery fish versus rehabilitating wild populations. For example, if a particular stock of hatchery fish is more competitive than a stock of wild fish, stocking will cause greater damage to the wild stock than if the wild population recovered to the same total density. Conversely, such measures of the net effect of stocking hatchery fish, independent of density, would allow hatchery managers to evaluate the effects of different culture and release strategies on hatchery fish performance. Substitutive experiments would also be of interest to test specific hypotheses regarding environmental or genetic effects. For example, the competitive ability relative to wild fish of hatchery stocks obtained from local populations or hatchery fish from supplementation programs could be compared with that of more traditional hatchery stocks to evaluate their effect on wild populations. More research using substitutive designs will also be necessary to determine how general any differences in competitive ability are across populations and species.

An important caution is that competition experiments can be used to quantify the effect of hatchery fish on wild fish in the short term, but when used alone, they cannot determine if hatchery stocking will ultimately damage wild stocks. Even if hatchery fish are less competitive than wild fish, hatchery fish may gradually replace wild fish where they are stocked every year because there is no feedback via mortality on the number of hatchery fish added. When natural environmental fluctuations result in low wild fish abundance, hatchery releases are generally not reduced. A short-term numerical advantage of hatchery fish could overwhelm wild fish even if wild fish are more competitive. Although stocking hatchery fish may provide additional spawners that could help restore small wild populations (McMichael and Pearsons (1998) and references therein), the contribution of hatchery fish to rebuilding wild populations has not been sufficiently evaluated (reviewed by Fleming and Petersson (2001)). Furthermore, surviving hatchery fish can damage wild stocks through genetic dilution, mixed-stock exploitation problems, and disease transmission, even if, on average, they are less competitive than wild fish. Recent studies indicate that stocking could ultimately reduce total fish populations because hatchery fish have negative effects on wild fish survival but also exhibit low survival themselves (McGinnity et al. 1997; Fleming et al. 2000; Einum and Fleming 2001). Measuring solely the strength of competition between wild and hatchery fish will not determine whether stocking is harmful to wild fish, but it will help managers understand where the largest ecological threats lie.

Acknowledgements

We thank B. Berejikian, I. Fleming, C. Myrick, T. Pearsons, S. Riley, J. Scheurer, C. Tatara, M. Unwin, G. White, and an anonymous reviewer for comments that improved the manu-

© 2003 NRC Canada

script. Funding for this research was provided by the U.S. Bureau of Reclamation (Cooperative Agreement 00-FC-81-0202), administered by B. Holt, R. Jackson, and D. Weigmann. We thank C. Liston and M. Stodolski for initiating funding.

References

Adelman, H.M., and Bingham, J.L. 1955. Winter survival of hatchery-reared and native brook trout. Prog. Fish. Cult. **17**: 177–180.

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. **113**: 1–32.

Bams, R.A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. **24**: 1117–1153.

Beamish, R.J., Thomson, B.L., and McFarlane, G.A. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. Trans. Am. Fish. Soc. **121**: 444–455.

Beamish, R.J., Mahnken, C., and Neville, C.M. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. ICES J. Mar. Sci. **54**: 1200–1215.

Berejikian, B.A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. Can. J. Fish. Aquat. Sci. **52**: 2476–2482.

Berejikian, B.A., Mathews S.B., and Quinn, T.P. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. Can. J. Fish. Aquat. Sci. **53**: 2004–2014.

Berejikian, B.A., Tezak, E.P., Schroder, S.L., Knudsen, C.M., and Hard, J.J. 1997. Reproductive behavioral interactions between wild and captively reared coho salmon (*Oncorhynchus kisutch*). ICES J. Mar. Sci. **54**: 1040–1050.

Berejikian, B.A., Tezak, E.P., Schroder, S.L., Flagg, T.A., and Knudsen, C.M. 1999. Competitive differences between newly emerged offspring of captive-reared and wild coho salmon. Trans. Am. Fish. Soc. **128**: 832–839.

Berg, S., and Jorgensen, J. 1991. Stocking experiments with 0+ and 1+ trout parr, *Salmo trutta* L., of wild and hatchery origin: 1. Post-stocking mortality and smolt yield. J. Fish Biol. **39**: 151–169.

Birch, L.C. 1957. The meanings of competition. Am. Nat. **91**: 5–18.

Bjornn, T.C. 1978. Survival, production, and yield of trout and chinook salmon in the Lemhi River, Idaho. Idaho Department of Fish and Game Federal Aid to Fish Restoration Project F-49-R. Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow, Bulletin No. 27.

Blaxter, J.H.S. 1975. Reared and wild fish — how do they compare? Proceedings of the 10th European symposium on marine biology, Ostend Belgium, September 17–23, 1975. Universa Press, Wetteren, Belgium.

Bohlin, T,L., Sundström, F., Johnsson, J.I., Höjesjö, J., and Pettersson, J. 2002. Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. J. Anim. Ecol. **71**: 683–692.

Braunnas, E. 1995. First access to territorial space and exposure to strong predation pressure: a conflict in early emerging Atlantic salmon (*Salmo salar* L.) fry. Evol. Ecol. **9**: 411–420.

Brauner, C.J., Iwama, G.K., and Randall, D.J. 1994. The effect of short-duration seawater exposure on the swimming performance of wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) during smoltification. Can. J. Fish. Aquat. Sci. **51**: 2188–2194.

Busack, C.A., and Currens, K.P. 1995. Genetic risks and hazards in hatchery operations: fundamental concepts and issues. *In* Uses and effects of cultured fishes in aquatic ecosystems. *Edited by* H.L. Schramm and R.G. Piper. Am. Fish. Soc. Symp. 15, Bethesda, Md. pp. 71–80.

Campton, D.E., and Johnston, J.M. 1985. Electrophoretic evidence for a genetic admixture of native and nonnative rainbow trout in the Yakima River, Washington. Trans. Am. Fish. Soc. **114**: 782–793.

Chandler, G.L., and Bjornn, T.C. 1988. Abundance, growth, and interactions of juvenile steelhead relative to time of emergence. Trans. Am. Fish. Soc. **117**: 432–443.

Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. **19**: 1047–1080.

Chilcote, M.W., Leider, S.A., and Loch, J.J. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Trans. Am. Fish. Soc. **115**: 726–735.

Clady, M.D. 1973. A competition and fish cultural study of rainbow trout — a literature review. Oregon State Game Commission Project No. F-94-R-1. Oregon State Wildlife Commission, Portland, Oregon.

Collis, K., Beaty, R.E., and Crain, B.R. 1995. Changes in catch rate and diet of northern squawfish associated with the release of hatchery-reared juvenile salmonids in a Columbia River reservoir. N. Am. J. Fish. Manag. **15**: 346–357.

Cresswell, R.C. 1981. Post-stocking movements and recapture of hatchery-reared trout released into flowing waters — a review. J. Fish Biol. **18**: 429–442.

Cutts, C.J., Bremis, B., Metcalfe, N.B., and Taylor, A.C. 1999. Prior residence, territory quality and life-history strategies in juvenile Atlantic salmon (*Salmo salar* L.). J. Fish. Biol. **55**: 784–794.

Deverill, J.I., Adams, C.E., and Bean, C.W. 1999. Prior residence, aggression, and territory acquisition in hatchery-reared and wild brown trout. J. Fish Biol. **55**: 868–875.

Dickson, T.A., and MacCrimmon, H.R. 1982. Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. Can. J. Fish. Aquat. Sci. **39**: 1453–1458.

Donnelly, W.A., and Whoriskey, F.G. 1991. Background-color acclimation of brook trout for crypsis reduces risk of predation by hooded mergansers *Lophodytes cucullatus*. N. Am. J. Fish. Manag. **11**: 206–211.

Doyle, R.W., and Talbot, A.J. 1986. Artificial selection on growth and correlated selection on competitive behaviour in fish. Can. J. Fish. Aquat. Sci. **43**: 1059–1064.

Egglishaw, H.J., and Shackley, P.E. 1980. Survival and growth of salmon, *Salmo salar* (L.), planted in a Scottish stream. J. Fish Biol. **16**: 565–584.

Einum, S., and Fleming, I.A. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. J. Fish Biol. **50**: 634–651.

Einum, S., and Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proc. R. Soc. Lond. B, **266**: 2095–2100.

Einum, S., and Fleming, I.A. 2001. Implications of stocking: ecological interactions between wild and released salmonids. Nordic J. Freshw. Res. **75**: 56–70.

Elliott, J.M. 1975. Weight of food and time required to satiate brown trout (*Salmo trutta*). Freshw. Biol. **5**: 51–64.

Ersbak, K., and Haase, B.L. 1983. Nutritional deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brook trout. N. Am. J. Fish. Manag. **3**: 142–151.

© 2003 NRC Canada

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**: 441–451.

Fausch, K.D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Can. J. Fish. Aquat. Sci. **45**: 2238–2246.

Fausch, K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 218–231.

Fausch, K.D., Taniguchi, Y., Nakano, S., Grossman, G.D., and Townsend, C.R. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecol. Appl. **11**: 1438–1454.

Fenderson, O.C., and Carpenter, M.R. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (*Salmo salar* L.). Anim. Behav. **19**: 439–447.

Fenderson, O.C., Everhart, W.H., and Muth, K.M. 1968. Comparative agonistic and feeding behaviour of hatchery reared and wild salmon in aquaria. J. Fish. Res. Board Can. **25**: 1–14.

Flagg, T.A., Waknitz, F.W., Maynard, D.J., Milner, G.B., and Mahnken, C.V.W. 1995. The effect of hatcheries on native coho salmon populations in the lower Columbia River. *In* Uses and effects of cultured fishes in aquatic ecosystems. *Edited by* H.L. Schramm and R.G. Piper. Am. Fish. Soc. Symp. 15, Bethesda, Md. pp. 366–375.

Fleming, I.A., and Einum, S. 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES J. Mar. Sci. **54**: 1051–1063.

Fleming, I.A., and Gross, M.R. 1989. Evolution of adult female life history and morphology in a Pacific salmon (Coho: *Oncorhynchus kisutch*). Evolution, **43**: 141–157.

Fleming, I.A., and Gross, M.R. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecol. Appl. **3**: 230–245.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution, **48**: 637–657.

Fleming, I.A., and Petersson, E. 2001. The ability of released, hatchery salmonids to breed and contribute to the natural productivity of wild populations. Nord. J. Freshw. Res. **75**: 71–78.

Fleming, I.A., Jonsson, B., and Gross, M.R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can. J. Fish. Aquat. Sci. **51**: 2808–2824.

Fleming, I.A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. Behav. Ecol. **8**: 470–480.

Fleming, I.A., Hindar, K., Mjolnerod, I.B., Jonsson, B., Balstad, T., and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proc. R. Soc. Lond. B, **267**: 1517–1523.

Fleming, I.A., Agustsson, T., Finstad, B., Johnsson, J.I., and Björnsson, B.T. 2002. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **59**: 1323–1330.

Flick, W.A., and Webster, D.A. 1964. Comparative first year survival and production in wild and domestic strains of brook trout, *Salvelinus fontinalis*. Trans. Am. Fish. Soc. **93**: 58–69.

Fresh, K.L. 1997. The role of competition and predation in the decline of Pacific salmon and steelhead. *In* Pacific salmon and their ecosystems: status and future options. *Edited by* D.J. Stouder, P.A. Bisson, R.J. Naiman, and M.G. Duke. Chapman and Hall, New York. pp. 245–275.

Glova, G.J., and Field-Dodgson, M.S. 1995. Behavioral interaction between chinook salmon and brown trout juveniles in a simulated stream. Trans. Am. Fish. Soc. **124**: 194–206.

Gowan, C., and Fausch, K.D. 2002. Why do foraging salmonids move during summer? Environ. Biol. Fishes, **64**: 139–13.

Grant, J.W.A. 1993. Whether or not to defend? The influence of resource distribution. *In* Behavioural ecology of fishes. *Edited by* F.A. Huntingford and P. Torricelli. Harwood Academic Publishers, Chur, Switzerland. pp. 137–153.

Greene, D.M. 1964. A comparison of stamina of brook trout from wild and domestic parents. Trans. Am. Fish. Soc. **93**: 96–100.

Gross, M.R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1) :131–144.

Hansen, L.P., and Jonsson, B. 1985. Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the River Imsa, Norway. Aquaculture, **45**: 237–248.

Hartman, G.F., Andersen, B.C., and Scrivener, J.C. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. Can. J. Fish. Aquat. Sci. **39**: 588–597.

Healey, M.C., and Reinhardt, U. 1995. Predator avoidance in naïve and experienced juvenile chinook salmon and coho salmon. Can. J. Fish. Aquat. Sci. **52**: 614–622.

Hilborn, R., and Eggers, D. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Trans. Am. Fish. Soc. **129**: 333–350.

Hillman, T.W., and Mullan, J.W. 1989. Effect of hatchery releases on the abundance and behavior of wild juvenile salmonids. *In* Summer and winter ecology of juvenile chinook salmon and steelhead trout in the Wenatchee River, Washington. Don Chapman Consultants, Boise, Idaho. pp. 266–285.

Hindar, K., Ryman, N., and Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. **48**: 945–957.

Hjort, R.C., and Schreck, C.B. 1982. Phenotypic differences among stocks of hatchery and wild coho salmon, *Oncorhynchus kisutch*, in Oregon, Washington, and California. Fish. Bull. **80**: 105–119.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **45**: 502–515.

Hughes, N.F. 1992. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **49**: 1999–2008.

Hume, J.M.B., and Parkinson, E.A. 1987. Effect of stocking density on the survival, growth, and dispersal of steelhead trout fry (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. **44**: 271–281.

Huntingford, F.A., and Garcia De Leaniz, C. 1997. Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. J. Fish Biol. **51**: 1009–1014.

Jenkins, T.M. 1971. Role of social behavior in dispersal of introduced rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **28**: 1019–1027.

Johnson, J.H., McKeon, J.F., and Dropkin, D.S. 1996. Comparative diets of hatchery and wild Atlantic salmon smolts in the Merrimack River. N. Am. J. Fish. Manag. **16**: 440–444.

Johnsson, J.I., and Abrahams, M.V. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhunchus mykiss*): an experimental study. Can J. Fish. Aquat. Sci. **48**: 243–247.

© 2003 NRC Canada

Johnsson, J.I., and Björnsson, B.Th. 1994. Growth hormone increases growth rate, appetite and dominance in juvenile rainbow trout, *Oncorhynchus mykiss*. Anim. Behav. **48**: 177–186.

Johnsson, J., Nobbelin, I.F., and Bohlin, T. 1999. Territorial competition among wild brown trout fry: effects of ownership and body size. J. Fish Biol. **54**: 469–472.

Johnsson, J.I., Petersson, E., Jonsson, E., Björnsson, B.T., and Jarvi, T. 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. Can. J. Fish. Aquat. Sci. **53**: 1546–1554.

Johnsson, J.I., Höjesjö, J., and Fleming, I.A. 2001. Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon. Can. J. Fish. Aquat. Sci. **58**: 788–794.

Kallio-Nyberg, I., and Koljonen, M.L. 1997. The genetic consequence of hatchery-rearing on life-history traits of Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. Aquaculture, **153**: 207–224.

Keenleyside, M.H.A., and Yamamoto, F.T. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour, **19**: 139–169.

Leider, S.A., Hulett, P.L., Lock, J.J., and Chilcote, M.W. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. Aquaculture, **88**: 239–252.

Levin, P.S., Zabel, R.W., and Williams, J.G. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proc. R. Soc. Lond. B. Biol. Sci. **268**: 1153–1158.

Marnell, L.F. 1985. Impacts of hatchery stocks on wild fish populations. *In* Fish culture in fisheries management. *Edited by* R.H. Stroud. Am. Fish. Soc. Fish Culture Section and Fisheries Management Section, Bethesda, Md. pp. 339–348.

Martel, G., and Dill, L.M. 1993. Feeding and aggressive behaviours in juvenile coho salmon (*Oncorhynchus kisutch*) under chemically-mediated risk of predation. Behav. Ecol. Sociobiol. **32**: 365–370.

Mason, J.C., and Chapman, D.W. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Board Can. **22**: 173–190.

Mason, J.W., Brynildson, O.M., and Degurse, P.E. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Trans. Am. Fish. Soc. **96**: 313–319.

Maynard, D.J., Flagg, T.A., and Mahnken, C.V.W. 1995. A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids. *In* Uses and effects of cultured fishes in aquatic ecosystems. *Edited by* H.L. Schramm and R.G. Piper. Am. Fish. Soc. Symp. 15, Bethesda, Md. pp. 307–314.

Maynard, D.J., McDowell, G.C., Tezak, E.P., and Flagg, T.A. 1996. Effect of diets supplemented with live food on the foraging behavior of cultured fall chinook salmon. Prog. Fish-Cult. **58**: 187–191.

McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T., and Ferguson, A. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES J. Mar. Sci. **54**: 998–1008.

McIntyre, J.D., and Reisenbichler, R.R. 1986. A model for selecting harvest fraction for aggregate populations of hatchery and wild anadromous salmonids. *In* Fish culture in fisheries management. *Edited by* R.H. Stroud. Am. Fish. Soc. Fish Culture Section and Fisheries Management Section, Bethesda, Md. pp. 179–189.

McLaren, J.B. 1979. Comparative behavior of hatchery-reared and wild brown trout and its relation to intergroup competition in a stream. Ph.D. dissertation, Pennsylvania State University, University Park.

McMichael, G.A., and Pearsons, T.N. 1998. Effects of wild juvenile spring chinook salmon on growth and abundance of wild rainbow trout. Trans. Am. Fish. Soc. **127**: 261–274.

McMichael, G.A., Sharpe, C.S., and Pearsons, T.N. 1997. Effects of residual hatchery-reared steelhead on growth of wild rainbow and spring chinook salmon. Trans. Am. Fish. Soc. **126**: 230–239.

McMichael, G.A., Pearsons, T.N., and Leider, S.A. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. N. Am. J. Fish. Manag. **19**: 948–956.

McMichael, G.A., Pearsons, T.N., and Leider, S.A. 2000. Minimizing ecological impacts of hatchery-reared juvenile steelhead trout on wild salmonids in a Yakima Basin watershed. *In* Sustainable fisheries management: Pacific salmon. *Edited by* E.E. Knudsen, C.R. Steward, D.D. MacDonald, J.E. Williams, and D.W. Reiser. Lewis Publishers, Boca Raton, Fla. pp. 365–380.

Mead, R.W., and Woodall, W.L. 1968. Comparison of sockeye salmon fry produced by hatcheries, artificial channels, and natural spawning areas. International Pacific Salmon Fisheries Commission Progress Report No. 20, New Westminster, British Columbia.

Mesa, M.G. 1991. Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. Trans. Am. Fish. Soc. **120**: 723–727.

Metcalfe, N.B. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for budgets and growth rates. J. Fish Biol. **28**: 525–531.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. J. Fish Biol. **41**(Suppl. B): 93–99.

Miller, R.B. 1955. Trout management research in Alberta. *In* Transactions of the 20th North American Wildlife Conference, 14–16 March. The Wildlife Management Institute, Washington, D.C. pp. 242–252.

Miller, R.B. 1958. The role of competition in the mortality of hatchery trout. J. Fish. Res. Board Can. **15**: 27–45.

Miller, R.B. 1962. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Trans. Am. Fish. Soc. **83**: 120–130.

Mortensen, E. 1977. The population dynamics of young trout (*Salmo trutta* L.) in a Danish brook. J. Fish Biol. **10**: 23–33.

Moyle, P.B. 1969. Comparative behavior of young brook trout of domestic and wild origin. Prog. Fish-Cult. **31**: 51–56.

Needham, P.R., and Slater, D.W. 1944. Survival of hatchery-reared brown and rainbow trout as affected by wild trout populations. J. Wildl. Manag. **8**: 22–36.

Nickelson, T.E., Solazzi, M.F., and Johnson, S.L. 1986. Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. Can. J. Fish. Aquat. Sci. **43**: 2443–2449.

Nielsen, J.L. 1994. Invasive cohorts — impacts of hatchery-reared coho salmon on the trophic, developmental and genetic ecology of wild stocks. *In* Theory and application in fish feeding ecology. *Edited by* D.J. Stouder, K.L. Fresh, and R. Feller. University of South Carolina Press, Columbia, S.C. pp. 361–385.

Noakes, D.J., Beamish, R.J., Sweeting, R., and King, J. 2000. Changing the balance: interactions between hatchery and wild Pacific coho salmon in the presence of regime shifts. North Pac. Anadromous Fish Comm. Bull. **2**: 155–163.

O'Connor, K.I., Metcalfe, N.B., and Taylor, A.C. 2000. The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (*Salmo salar*). Behav. Ecol. **11**: 13–18.

© 2003 NRC Canada

Olla, B.L., and Davis, M.W. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture, **76**: 209–214.

Olla, B.L., Davis, M.W., and Ryer, C.H. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquacult. Fish. Manag. **25**(Suppl. 1): 19–34.

Olla, B.L., Davis, M.W., and Ryer, C.H. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. Bull. Mar. Sci. **62**: 531–550.

Pearcy, W.G. 1997. Salmon production in changing ocean domains. *In* Pacific salmon and their ecosystems: status and future options. *Edited by* D.J. Stouder, P.A. Bisson, R.J. Naiman, and M.G. Duke. Chapman and Hall, New York. pp. 331–352.

Peery, C.A., and Bjornn, T.C. 1996. Small-scale investigations into chinook salmon. Supplementation strategies and techniques: 1992–1994. Bonneville Power Administration Technical Rep. No. 96-3, Portland, Oregon.

Petersson, E., Jarvi, T., Steffner, N.G., and Ragnarsson, B. 1996. The effect of domestication on some life history traits of sea trout and Atlantic salmon. J. Fish Biol. **48**: 776–791.

Petrosky, C.E., and Bjornn, T.C. 1988. Response of wild rainbow (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) to stocked rainbow trout in fertile and infertile stream. Can. J. Fish. Aquat. Sci. **45**: 2087–2105.

Phillips, A.M. 1957. A chemical comparison of hatchery and wild brook trout. Prog. Fish. Cult. **19**: 19–25.

Piggins, P.J., and Mills, C.P.R. 1985. Comparative aspects of the biology of naturally produced and hatchery-reared Atlantic salmon smolts (*Salmo salar* L.). Aquaculture, **45**: 321–333.

Pollard, H.A., and Bjornn, T.C. 1973. The effects of angling and hatchery trout on the abundance of juvenile steelhead trout. Trans. Am. Fish. Soc. **102**: 745–752.

Quinn, T.P., and Peterson, N.P. 1996. The influence of habitat complexity and fish size on overwinter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Can. J. Fish. Aquat. Sci. **53**: 1555–1564.

Reinhardt, U.G., Yamamoto, T., and Nakano, S. 2001. Effects of body size and predators on intracohort competition in wild and domesticated juvenile salmon in a stream. Ecol. Res. **16**: 327–334.

Reisenbichler, R.R., and McIntyre, J.D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board Can. **34**: 123–128.

Reisenbichler, R.R., and Rubin, S.P. 1999. Genetic changes from artificial propagation of Pacific salmon affect productivity and viability of supplemented populations. ICES J. Mar. Sci. **56**: 459–466.

Rhodes, J.S., and Quinn, T.P. 1998. Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. J. Fish Biol. **53**: 1220–1230.

Rhodes, J.S., and Quinn, T.P. 1999. Comparative performance of genetically similar hatchery and naturally reared juvenile coho salmon in streams. N. Am. J. Fish. Manag. **19**: 670–677.

Richards, C., and Cernera, P.J. 1989. Dispersal and abundance of hatchery-reared and naturally spawned juvenile chinook salmon in an Idaho stream. N. Am. J. Fish. Manag. **9**: 345–351.

Ritter, J.A., and MacCrimmon, H.R. 1973. Influence of environmental experience on response of yearling rainbow trout (*Salmo gairdneri*) to a black and white substrate. J. Fish. Res. Board Can. **30**: 1740–1742.

Rosenau, M.L., and McPhail, J.D. 1987. Inherited differences in agonistic behavior between two populations of coho salmon. Trans. Am. Fish. Soc. **116**: 646–654.

Ruzzante, D.E. 1994. Domestication effects on aggressive and schooling behavior in fish. Aquaculture, **120**: 1–24.

Salonius, K., and Iwama, G.K. 1993. Effects of early rearing environment on stress response, immune function, and disease resistance in juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*). Can. J. Fish. Aquat. Sci. **50**: 759–766.

Schuck, H.A. 1948. Survival of hatchery trout in streams and possible methods of improving the quality of hatchery trout. Prog. Fish. Cult. **10**: 3–14.

Seegrist, D.W., and Gard, R. 1972. Effects of floods on trout in Sagehen Creek, California. Trans. Am. Fish. Soc. **101**: 478–482.

Seelbach, P.W. 1987. Smolting success of hatchery-raised steelhead planted in a Michigan tributary of Lake Michigan. N. Am. J. Fish. Manag. **7**: 223–231.

Seelbach, P.W., and Whelan, G.E. 1988. Identification and contribution of wild and hatchery steelhead stocks in Lake Michigan tributaries. Trans. Am. Fish. Soc. **117**: 444–451.

Shrimpton, M.J., Bernier, N.J., Iwama, G.K., and Randall, D.J. 1994. Differences in measurements of smolt development between wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) before and after saltwater exposure. Can. J. Fish. Aquat. Sci. **51**: 2170–2178.

Siikavuopio, S.I., Baardvik, B.M., and Jobling, M. 1996. Domestication effects on fin nipping, survival and growth in hatchery-reared arctic charr, *Salvelinus alpinus* (L.), in competition with wild conspecifics. Aquacult. Res. **27**: 205–211.

Smirnov, B.P., Chebanova, V.V., and Vvedenskaya, T.V. 1994. Adaptation of hatchery-rased chum salmon, *Oncohynchus keta*, and chinook salmon, *O. tshawytscha*, to natural feeding and effects of starvation. J. Icthyol. **34**: 96–106.

Sosiak, A.J., Randall, R.G., and McKenzie, J.A. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. J. Fish. Res. Board Can. **36**: 1408–1412.

Steward, C.R., and Bjornn, T.C. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: a synthesis of published literature. Tech. Rep. No. 90-1 for The Office of Information Transfer, U.S. Fish and Wildlife Service, Dworshak Fisheries Assistance Office, U.S. Fish and Wildlife Service, and Bonneville Power Administration.

Swain, D.P., and Riddell, B.E. 1990. Variation in agonistic behaviour between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. **47**: 566–571.

Swain, D.P., Riddell, B.E., and Murray, C.B. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. Can. J. Fish. Aquat. Sci. **48**: 1783–1791.

Symons, E.K. 1969. Greater dispersal of wild compared with hatchery-reared juvenile Atlantic salmon released in streams. J. Fish. Res. Board Can. **26**: 1867–1876.

Taylor, E.B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. Prog. Fish. Cult. **48**: 171–176.

Taylor, E.B., and Larkin, P.A. 1986. Current response and agonistic behavior in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. Can. J. Fish. Aquat. Sci. **43**: 565–573.

Thuemler, T. 1975. Fish the blue ribbon streams. Wisconsin Conserv. Bull. **40**: 16–17.

Underwood, T. 1986. The analysis of competition by field experiments. *In* Community ecology: pattern and process. *Edited by* J. Kikkawa and D.J. Anderson. Blackwell Scientific Publications, Palo Alto, Calif. pp. 240–268.

© 2003 NRC Canada

Unwin, M.J., and Glova, G.J. 1997. Changes in life history parameters in a naturally spawning population of chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish. Can. J. Fish. Aquat. Sci. **54**: 1235–1245.

Unwin, M.J., and Lucas, D.H. 1993. Scale characteristics of wild and hatchery chinook salmon (*Oncorhynchus tshawytscha*) in the Rakaia River, New Zealand, and their use in stock identification. Can. J. Fish. Aquat. Sci. **50**: 2475–2484.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Trans. Am. Fish. Soc. **89**: 35–52.

Vincent, R.E. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. N. Am. J. Fish. Manag. **7**: 91–105.

Volpe, J.P., Anholt, B.R., and Glickman, B.W. 2001. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. Can. J. Fish. Aquat. Sci. **58**: 197–207.

Wales, J.H. 1954. Relative survival of hatchery and wild trout. Prog. Fish. Cult. **16**: 125–127.

Weiss, S., and Schmutz, S. 1999. Performance of hatchery-reared brown trout and their effects on wild fish in two small Austrian streams. Trans. Am. Fish. Soc. **128**: 302–316.

White, R.J., Karr, J.R., and Nehlsen, W.N. 1995. Better roles for fish stocking in aquatic resource management. *In* Uses and effects of cultured fishes in aquatic ecosystems. *Edited by* H.L. Schramm and R.G. Piper. Am. Fish. Soc. Symp. 15, Bethesda, Md. pp. 527–547.

Winton, J., and Hilborn, R. 1994. Lessons from supplementation of chinook salmon in British Columbia. N. Am. J. Fish. Manag. **14**: 1–13.

Woodward, C.C., and Strange, R.J. 1987. Physiological stress responses in wild and hatchery-reared rainbow trout. Trans. Am. Fish. Soc. **116**: 574–579.

Youngson, A.F., and Verspoor, E. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 153–160.

© 2003 NRC Canada

ERRATUM / ERRATUM

Erratum: Implications of life-history invariants for biological reference points used in fishery management

Erik H. Williams and Kyle W. Shertzer

Ref.: Can. J. Fish. Aquat. Sci. **60**: 710–720 (2003).

On page 710, in the third paragraph, errors were incorporated during page production. The corrected paragraph is reprinted below.

One common BRP relates the target or limit fishing mortality rate (F') to the natural mortality rate (M) by some constant c_1 such that $F' = c_1M$. The rationale of this "M-based" BRP is that stocks with higher M tend to have higher production rates and can therefore sustain increased fishing. It was originally proposed that $F' = M$ as a proxy for the maximum sustainable fishing rate (F_{MSY}). Current applications usually take a more risk-averse strategy by considering M an upper bound and using $c_1 < 1$ (Quinn and Deriso 1999). For example, groundfish harvest policies for the Pacific and North Pacific (PFMC) councils use $F' = 0.75M$ in cases in which limited data do not allow reliable estimation of F_{MSY} (Witherell and Ianelli 1997; PFMC 2001).

We apologize for any inconvenience this may have caused.

Received 28 July 2003. Accepted 4 September 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 30 September 2003.
J17059E

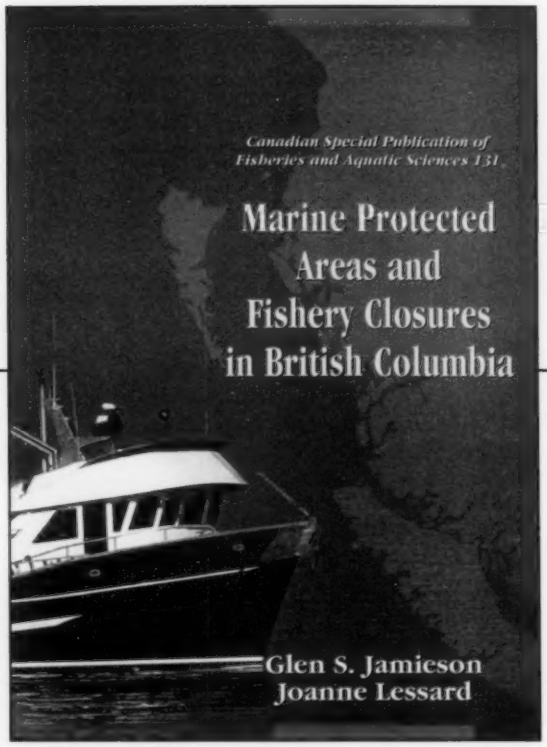
E.H. Williams[1] **and K.W. Shertzer.** Center for Coastal Fisheries and Habitat Research, National Oceanic and Atmospheric Administration, 101 Pivers Island Road, Beaufort, NC 28516, U.S.A.

[1]Corresponding author (e-mail: Erik.Williams@noaa.gov).

 doi: 10.1139/F03-099 © 2003 NRC Canada

Marine Protected Areas and Fisheries Closures in British Columbia

By/par Glen S. Jamieson and/et Joanne Lessard


Canadian Special Publication of Fisheries and Aquatic Sciences 131
Marine Protected Areas and Fishery Closures in British Columbia
Glen S. Jamieson
Joanne Lessard

$69.95/69,95 $

Other countries $69.95 US
À l'étranger 69,95 $US

Softcover / Edition brochée
414 pages
ISBN 0-660-17788-9 ISSN 0706-6481
NRC No./N° du CNRC 42846
(Can. Spec. Publ. Fish. Aquat. Sci. No. 131)

Orders may be submitted by mail or fax to: Les commandes peuvent être soumises par courrier ou par télécopieur à :

Order Office/Bureau des commandes

NRC Research Press/Presses scientifique du CNRC
National Research Council/Conseil national de recherches
Ottawa, ON K1A 0R6, Canada
Telephone/Téléphone : (613) 990-2254
Fax/Télécopieur : (613) 952-7656
E-mail: research.press@nrc.ca
Courriel : presses.scientifiques@cnrc.ca
Website: http://researchpress.nrc.ca
Site web : http://pressesscientifiques.cnrc.ca

PLEASE PRINT/LETTRES MOULÉES

☐ Payment enclosed / Paiement inclus ☐ Charge to/ Imputer à ☐ Visa ☐ MasterCard ☐ AMEX

Account no./N° de compte | Expiry date/Date d'expiration

Name/Nom

Signature

Address/Adresse

City/Ville | Province

Postal code/Code postal | Country/Pays

Telephone/Téléphone | Fax/Télécopieur

E-mail/courriel

Prepayment required unless order is accompanied by a purchase order number. Cheques or money orders should be made payable to : "Receiver General for Canada, Credit NRC". For all orders outside Canada, rates are in U.S. Dollars. All sales are final.
Les commandes doivent être payées d'avance à moins qu'elles ne soient accompagnées d'un numéro de bon de commande. Les chèques ou mandats doivent être libellés au « Receveur général du Canada, crédit du CNRC ». Toutes les ventes sont finales.

PERSPECTIVE

Edward D. Weber and Kurt D. Fausch **1018–1036** Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition

ERRATUM

Erik H. Williams and Kyle W. Shertzer **1037** Erratum: Implications of life-history invariants for biological reference points used in fishery management

National Research Council Canada
Ottawa, Canada K1A 0R6

Conseil national de recherches Canada
Ottawa, Canada K1A 0R6

Postage paid at Ottawa
Publications mail
Registration No. 40062591

Port payé à Ottawa
Poste-publication
Enregistrement n° 40062591

USPS periodical postage paid at Champlain, N.Y.

Canadian Journal of Fisheries and Aquatic Sciences

Volume 60, Number 8, August 2003

Journal canadien des sciences halieutiques et aquatiques

Volume 60, numéro 8, août 2003

	ARTICLES	ARTICLES
Douglas P. Swain and Elmer J. Wade	**897–909**	Spatial distribution of catch and effort in a fishery for snow crab (*Chionoecetes opilio*): tests of predictions of the ideal free distribution
Carol Seals Price and Carl B. Schreck	**910–918**	Stress and saltwater-entry behavior of juvenile chinook salmon (*Oncorhynchus tshawytscha*): conflicts in physiological motivation
Steven Declerck, Vanessa Geenens, Nicole Podoor, José Maria Conde Porcuna, and Luc De Meester	**919–928**	Intraspecific density dependence in the dynamics of zooplankton under hypertrophic conditions
Myron A. Peck, Lawrence J. Buckley, and David A. Bengtson	**929–937**	Energy losses due to routine and feeding metabolism in young-of-the-year juvenile Atlantic cod (*Gadus morhua*)
James E. Garvey and Elizabeth A. Marschall	**938–948**	Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation
Valerio Matozzo, Luisa Da Ros, Loriano Ballarin, Francesca Meneghetti, and Maria Gabriella Marin	**949–958**	Functional responses of haemocytes in the clam *Tapes philippinarum* from the Lagoon of Venice: fishing impact and seasonal variations
P.J. Dillon, B.J. Clark, L.A. Molot, and H.E. Evans	**959–970**	Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes
Kevin S. McCann, Louis W. Botsford, and Alan Hasting	**971–985**	Differential response of marine populations to climate forcing
Theodore Castro-Santos and Alex Haro	**986–996**	Quantifying migratory delay: a new application of survival analysis methods
Robin J. Wyatt	**997–1006**	Mapping the abundance of riverine fish populations: integrating hierarchical Bayesian models with a geographic information system (GIS)
Joshua J. Latterell, Robert J. Naiman, Brian R. Fransen, and Peter A. Bisson	**1007–1017**	Physical constraints on trout (*Oncorhynchus* spp.) distribution in the Cascade Mountains: a comparison of logged and unlogged streams

Continued on inside back cover / Suite au verso

Canada

Printed in Canada by / Imprimé au Canada par
University of Toronto Press Inc.
Page production by / Mise en page par
NRC Research Press / Presses scientifiques du CNRC

0706-652X(200308)60:8;1-#